

1 A general framework for estimating species  
2 contribution to community changes

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8 **Abstract**

9 Community Weighted Means are widespread and valuable tools for  
10 describing ongoing changes in natural communities. However, these ag-  
11 gregated community-level indices ignore interspecific variability, and are  
12 therefore limited to descriptive results. There is a need for a general  
13 framework relating changes in community and population dynamics inte-  
14 grating species-specific variations. We build upon Community Weighted  
15 Means to propose an extended framework using simple, yet informative,  
16 metrics (means and variances) of community changes in structure and  
17 composition while revealing species contributions to those changes.

18 We apply this approach to the reshuffling of common birds communities  
19 in the French Mediterranean area between 2001 and 2012. The empirical  
20 analysis confirms that our approach helps understanding the species dy-  
21 namic patterns that shape the changes at the community level and reveals

22 the key species responsible for directional changes in functional composi-  
23 tion.

24 Overall, this novel decomposition and interpretation of Community Weighted  
25 Means could shed some new light on the means and causes of community  
26 modifications in response to environmental changes across time and space.  
27 Moreover, it represents a crucial tool for assessing particular aspects of  
28 species-specific responses to environmental changes.

29  
30 Keywords: community ecology, community weighted means, func-  
31 tional biogeography, niche, interaction milieu, birds, global changes.

## 32 1 Introduction

33 Community ecologists working on global changes have faced the dilemma of ei-  
34 ther aggregating complex information using meaningful indices (such as species  
35 richness, diversity indices or more elaborated indices of community composi-  
36 tion) or working on single species information. A consequence of the tension  
37 between these two levels of information - community and species - is that which  
38 species contribute to explain changes in community diversity and composition,  
39 and how such contribution occurs, is often ignored. Conversely, studying indi-  
40 vidual species responses to environmental changes may not allow scaling up to  
41 community level responses, in particular because of the importance of species  
42 interactions in such responses.

43  
44 The challenge of linking community changes with individual species dynam-  
45 ics has contributed to divide empirical and conceptual global change studies  
46 in two main branches. On the one hand, community-level approaches have  
47 schematically focused on describing spatial and temporal trends in diversity  
48 and composition in space and time. In this context, species richness or diversity

49 indices are often used as integrative descriptors of the community (Mackey &  
50 Currie 2001) environmental changes, community structure and composition are  
51 expected to be modified depending on community assembly rules (Logue *et al.*  
52 2011). On the other hand, species-level approaches have broadly focused on how  
53 individual species occurrences or abundances are distributed along environmen-  
54 tal gradients. Following a disturbance, species abundances and distributions  
55 are expected to be altered according to the position and breadth of the species  
56 niche. For instance, climate change is expected to trigger range shifts of many  
57 species if those species are tracking the climate according to their specific tem-  
58 perature preference (Thomas *et al.* 2004).

59

60 While these two approaches have independently contributed to better de-  
61 scribe biodiversity responses to environmental changes, linking population and  
62 community-level dynamics remains a challenge (Walther *et al.* 2002). This limit  
63 was emphasized by a call for adopting a more functional view of community  
64 ecology, which would better describe how communities are shaped by explicit  
65 environmental gradients and how this is mediated by species traits (McGill  
66 *et al.* 2006). In this respect, beyond the importance to take functional differ-  
67 ences among species into account, the need to also account for differences within  
68 species has been emphasized as well (Violle *et al.* 2012). Indeed, if intra-species  
69 variability in a given trait is higher than inter-species variability, focusing on  
70 changes in functional richness and composition of communities using averaged  
71 value for each species can be meaningless.

72

73 To overcome these limits, two methodological approaches have been devel-  
74 oped that provide a description of community responses using trait rather  
75 than species - diversity. A first available approach integrating trait variability

76 within communities consists in defining communities functional structure as the  
77 distribution of species and their abundances in the functional space character-  
78 ized by multiple functional traits (Villger *et al.* 2008). This multidimensional  
79 approach allows the quantification of inter-species variability in the traits con-  
80 sidered. Therefore, two communities with similar functional richness but uneven  
81 distribution of individuals among functional traits and/or very original traits  
82 can be differentiated. The use of this multidimensional functional space based  
83 on species traits has emerged as a useful way to quantify expected changes in  
84 community structure after disturbances (Mouillot *et al.* 2013).

85  
86 Another approach consists in using community weighted means (hereafter,  
87 CWM) to describe community composition with respect to one given species-  
88 specific trait. CWM have been widely used in global change studies to address  
89 the question of community reshuffling in response to environmental perturba-  
90 tions. They have been applied to a variety of traits such as the mean of the  
91 realized thermal niche: Community Thermal Index (Devictor *et al.* 2008b; 2012;  
92 Princ & Zuckenberg 2015; Clavero *et al.* 2011; Godet *et al.* 2011; Jiguet *et al.*  
93 2011; Kampichler *et al.* 2012; Lindstrm *et al.* 2013; Barnagaud *et al.* 2012; 2013;  
94 Roth *et al.* 2014), other examples include the Mean Catch Temperature (Che-  
95 ung *et al.* 2013), the community weighted latitude (Dulvy *et al.* 2008), altitude  
96 (Clavero *et al.* 2011), specialization (Clavel *et al.* 2010) or Ellenberg averaged  
97 values (Lenoir *et al.* 2013). They have been applied to birds (Devictor *et al.*  
98 2008b; Princ & Zuckenberg 2015), butterflies (Roth *et al.* 2014; Devictor *et al.*  
99 2012), plants (Lenoir *et al.* 2013) and fish (Dulvy *et al.* 2008; Cheung *et al.*  
100 2013) communities.

101  
102 Although these two types approaches have clearly been useful to describe

103 general changes in species assemblages, they still mask species-specific dynam-  
104 ics. In particular, a change in functional space or CWM do not tell which species  
105 and traits have been lost or gained and whether it is driven by few key species  
106 or by the entire species pool. Moreover, integrating inter- versus intra-species  
107 variability is not explicitly considered. Overall, a simple general framework al-  
108 lowing to monitor changes in community and species dynamics while accounting  
109 for functional differences between and within species is missing. Yet, to shed  
110 lights on the processes responsible for observed community changes, knowing  
111 how much each individual species contributes, as well as the direction and mag-  
112 nitude of these contributions, might be relevant. For instance, following climate  
113 change, conservation implications would be very different if only two or three  
114 focal species are responsible for an observed change in a community-based in-  
115 dex. Further, assessing the contributions for meaningful functional groups (e.g.  
116 protected vs unprotected, competitive or not, exotic or resident) might be of  
117 interest to test ecological predictions or to help designing conservation plans.

118

119 Here, we propose a general framework, along with open source software  
120 to perform such analyses, to assess the contributions of species or group of  
121 species to CWM variations. We then introduce the community-weighted vari-  
122 ance (CWV) as a new functional diversity indicator and propose a way to com-  
123 pute species contributions to its variations. Finally, we present an application  
124 of this method to the French breeding bird survey.

## 125 2 Partition of Community Weighted Mean vari- 126 ations

### 127 2.1 An interaction milieu descriptor

128 Community Weighted Means (CWM) are a first order implementation of the  
129 interaction milieu paradigm (the pool of local strategies which shapes of the  
130 realised niche of a focal species, see McGill *et al.* (2006) for an extended defini-  
131 tion). They are the average of the local distribution of a trait in a community  
132 (i.e. the expected value of the trait if we take an individual at random from the  
133 community). Considering a community of  $N$  individuals,  $R$  species, with  $p_i$  the  
134 relative abundance of species  $i$  and  $t_i$  the mean value of the trait of species  $i$ ,  
135 the mean field estimator of the CWM is defined as:

$$CWM = \sum_{i=1}^R p_i t_i \quad (1)$$

136 CWM are community functional parameters (i.e. an aggregated indicators  
137 obtained from population level information, as defined in (Violle *et al.* 2007)).  
138 They can be seen as the simplest summary statistics of the interaction milieu.  
139 They are also not expected to depend on the species richness. They can be linked  
140 to more sophisticated, multi-trait analysis like hypervolume methods (Blonder  
141 *et al.* 2014). However, their simplicity (due to the use of a single trait) allows for  
142 easier biological interpretations. Ecosystem processes such as carbon fixation,  
143 resource consumption or denitrification can be driven by a few key traits (Reiss  
144 *et al.* 2009). For instance, a CWM built from plant height will be a descriptor  
145 of the mean light-grabbing strategy in this community. Thus, the study of a  
146 process goes through the selection of one or several relevant trait(s). Following  
147 a change in light availability, the previously mentioned CWM is expected to

148 increase if taller species colonize the assemblage.

149 By construction, CWM do not contain information about species-specific  
150 responses and functional diversity because of the averaging. Following our ex-  
151 ample, the increase in the plant height CWM does not inform about whether  
152 such an increase is due to an increased proportion of a few of the tallest plants  
153 or a collapse of small plants in the community. In other words, CWM are  
154 information-poor (i.e. incomplete) descriptors of complex distributions. More-  
155 over, they ignore the trait heterogeneity between and within species.

## 156 2.2 Species contributions

157 The lack of reliable way to quantify species contributions to a CWM trend  
158 (Jiguet *et al.* 2011; Davey *et al.* 2013) has highly limited the practical relevance  
159 and implementation of those indices since conservation policies are mostly based  
160 on species-specific measures. Recently, (Princ & Zuckerberg 2015) proposed a  
161 way to estimate species contributions to a CWM trend. This approach was  
162 inspired by a species jackknife method previously used on diversity indices (Davey  
163 *et al.* 2013): the linear trend of the indice is measured on both the whole dataset  
164 ( $\beta$ ) and the whole dataset but the focal species  $k$  ( $\beta_{i \notin k}$ ). This is done/repeated  
165 for all species in the data set. Each species' contribution  $C_k$  is then defined as:

$$C_k = \beta_{i \notin k} - \beta \quad (2)$$

166 We propose a direct expression for the specific contribution  $C_k$ . Because of  
167 the linear nature of the CWM with respect to the trend in relative abundance,  
168 this expression is exact if the trends are approximated by an ordinary least  
169 square regression of the index as a function of time. In this case, the contribution  
170 of species  $k$  is equal to the product of the linear trend of its relative abundance  
171 ( $\Delta p_k$ ) times its *functional originality*, defined by its mean difference to trait

172 values of the other species in the community ( $o_k = \overline{\theta_{i \neq k}} - \theta_k$ , see appendix A for  
 173 a demonstration):

$$C_k = \Delta p_k o_k \quad (3)$$

174 This expression highlights that the more original a species in its trait value  
 175 compared to the rest of the community, and the higher its relative abundance  
 176 trend, the higher its absolute contribution will be to the CWM trend. Further-  
 177 more, positive contributors are species for whom relative abundance trend and  
 178 originality have the same sign. Conversely, negative contributors are species  
 179 for which those quantities are of opposite sign. Going back to our example  
 180 where the trait considered is height, species contributions reveal which species  
 181 is contributing in each way to the change in average height: for instance, a ex-  
 182 ceptionally tall species that slightly increased in proportion or a group of slightly  
 183 smaller-than-average species that disappeared.

184

185 Using a slight modification of the expression of the species contribution in-  
 186 cluding the focal species ( $\Omega_i = \overline{\theta_{i=1}^R} - \theta_k$ ), the sum of the species contributions  
 187 is now the CWM variation (see appendix A for a demonstration):

$$C_k = \Delta p_k \Omega_k \quad (4)$$

and we now have

$$\sum_{k=1}^R C_k = \Delta CWM \quad (5)$$

188 Consequently, it makes sense to define the contribution of a group of species as  
 189 the sum of their species contributions. This opens the way to simple decompo-  
 190 sitions of a CWM variation according to, for instance, taxonomic or functional  
 191 groups of species. As an example, if  $A$  is a subset of species, we have:



$$\sum_{k \geq A} C_k + \sum_{k \leq A} C_k = \Delta CWM \quad (6)$$

192 Using this approach and following our example of plant size-based CWM, one  
 193 could segregate the contribution of C4 plants (or other distinction). Moreover,  
 194 a partition between positively and negatively contributing species would be  
 195 informative, all the more so as a further partition would be possible between  
 196 positive contributors that have a positively original trait value and a positive  
 197 relative abundance trend and the ones that have a negatively original trait value  
 198 and a negative relative abundance trend.

## 199 3 Community weighted variances

### 200 3.1 A functional diversity index

201 In the following, we go one step further by introducing the community weighted  
 202 variance (CWV) as a functional diversity indicator, and we propose a way to  
 203 compute species contributions to its variations. This extension of the community  
 204 weighted indices to variance is motivated by the fact that we need a diversity  
 205 index that is functional (to be linked to ecosystem processes), simple to compute  
 206 and interpret and complementary to the CWM.

207 The general formula for an unbiased estimator (using Bessel's correction for  
 208 small samples) of the variance of the distribution of a trait in a community using  
 209 a sample of  $N$  individuals,  $R$  species with  $p_i$  the relative abundance of species  
 210  $i$  and  $t_i$  the value of the trait of species  $i$  is:

$$CWV(t) = \frac{N}{N-1} \sum_{i=1}^R p_i (t_i - CWM)^2 \quad (7)$$

$$= \frac{N}{N-1} \left( \sum_{i=1}^R p_i t_i^2 - (CWM)^2 \right) \quad (8)$$

211 For a given trait, the CWV is a measure of the mean squared functional  
 212 originality. An increase in CWV means that the community is enriched in orig-  
 213 inal individuals. Conversely, a decrease in CWV is the sign that the community  
 214 experiences a loss of original individuals. Going on with our plant example, such  
 215 an index would allow addressing the question of whether there is an homoge-  
 216 nization in plant height. Note that the CWV takes into account the relative  
 217 species abundances as opposed to the local inter-species trait variance that has  
 218 been used in previous studies (Roth *et al.* 2014). As a result it gives a more  
 219 accurate image of the functional diversity in highly uneven communities.

220 The variation in CWV is a first way to refine a variation in CWM (Fig. 1) : if  
 221 an increase in CWM is linked to an increase in CWV, it means that the variation  
 222 in CWM is due to an increased weight in the community of species that have  
 223 a higher trait value (or an invasion of new high-valued species). Conversely, if  
 224 CWV decreases, it means that the increase in the mean is driven by losses in  
 225 species with a lower trait value. Thus, if the CWM and the CWV are correlated,  
 226 it means that variations in the mean are due to original individuals, whereas  
 227 if their are anti-correlated it means that this variation is due to unoriginal  
 228 individuals.

### 229 3.2 Species contributions

230 In analogy with what we proposed for the mean, we propose a decomposition  
 231 of a CWV variation that can be used to distinguish the relative contributions

232 of species or groups of species to the variation in the indices (see section A for  
 233 a proof. This formula is exact if we use the biased sample variance estimator or  
 234 if  $\frac{N}{N-1}$  is constant. We have:

$$\Delta CWW = \sum_{i=1}^R C_i \quad (9)$$

235 with:

$$C_i = \Delta p_i [\omega_i - S\Omega_i] \quad (10)$$

236 where  $S$  is the sum of the initial and final CWM,  $\Delta p_i$  is the relative abun-  
 237 dance variation of species  $i$ ,  $\omega_i$  its trait originality and  $\Omega_i$  its "variance original-  
 238 ity".

$$\omega_i = \frac{1}{R} \sum_{j=1}^R t_i^2 - t_j^2 \quad (11)$$

$$\Omega_i = \frac{1}{R} \sum_{j=1}^R t_i - t_j \quad (12)$$

$$S = CWM_i + CWM_f \quad (13)$$

$$(14)$$

### 239 3.3 Taking intra-species variation of a trait into account

240 It is noteworthy that our approach (as well as the hypervolume approach) is  
 241 easily generalized to take intra-species variability into account. Indeed, the  
 242 consideration of those measures has been showed to qualitatively change the  
 243 conclusions about assembly processes (Violle *et al.* 2012).

244 Firstly, the CWM will not be affected by the addition of the variance of  
 245 the trait (because of the linearity of the mean). However, the CWV expression

246 will be different since intraspecific trait variation increases the community wide  
 247 variance. If we only know the intraspecific variance, we can, as a first approxi-  
 248 mation, consider that the trait value follow a normal distribution with the same  
 249 mean ( $t_i$ ) and variance ( $\sigma_i^2$ ). Consequently, the community distribution of the  
 250 trait is a Gaussian mixture and its variance is given by (Frhwirth-Schnatter  
 251 2006) :

$$Var(t) = \frac{1}{R} \sum_{i=1}^R p_i (\sigma_i^2 + t_i^2) - CWM^2 \quad (15)$$

252 For species contributions,  $\omega_i$  becomes:

$$\omega_i = \frac{1}{R} \sum_{j=1}^R (t_i^2 + \sigma_i^2) - (t_j^2 + \sigma_j^2) \quad (16)$$

253 This however requires knowing trait value at the individual rather than at  
 254 the species level, and will not be illustrated in our case study because of the  
 255 lack of relevant data.

## 256 4 Case study : Community reshuffling of French 257 Mediterranean bird assemblages

### 258 4.1 Data

259 To investigate the informative power of the approach described in the previous  
 260 sections, we applied our analysis framework to the Mediterranean avifauna mon-  
 261 itored by the French Breeding Bird Survey (FBBS) between 2001 and 2012 (Jul-  
 262 liard *et al.* 2006). The FBBS is a large scale and long term monitoring program  
 263 in which volunteer skilled ornithologists count birds following a standardized  
 264 protocol at the same site, year after year since 2001 (Jiguet *et al.* 2012). Species  
 265 abundances were recorded inside 2km\*2km squares whose centroids were located

266 within a 10km radius around a locality specified by the volunteer. To improve  
267 the representation of the diversity of habitats countrywide (Veech *et al.* 2012),  
268 squares were randomly placed within the 10km buffer. On each site, volunteers  
269 carried out 10 point counts (5min each, separated by at least 300m) twice per  
270 spring within three weeks around the pivotal date of May 8th to ensure the de-  
271 tection of both early and late breeders. Counts were repeated at approximately  
272 the same date between years ( 7 days) and at dawn (within 14h after sunrise)  
273 by a unique observer. The maximum count per point for the two spring sessions  
274 was retained as an indication of point-level species abundance. We limited our  
275 study to sites belonging to the Mediterranean biogeographic domain because of  
276 the substantial environmental changes which occurred in this area during the  
277 period of study (Gazre *et al.* 2015).

## 278 4.2 Analysis

279 We applied our community analysis framework to this dataset to describe the  
280 temporal variation and the specific contributions to the CWM and CWV of  
281 two contrasted traits: the Species Thermal Index (STI, expressed in degree  
282 Celsius; [(Devictor *et al.* 2008a;b)]and the species average lifespan.The STI is  
283 an integrative species characteristic representing the thermal preference of each  
284 bird species.It corresponds to the average temperature experienced by a species  
285 across its geographic range during the breeding season. STI values were com-  
286 puted from 0.5 by 0.5 degree temperature grids (AprilJuly averages for the pe-  
287 riod 19502000; Worldclim data base, <http://www.worldclim.org>) coupled with  
288 species Western Palaearctic distributions at a 0.5 degree resolution from EBCC  
289 atlas of European breeding birds (Hagemeijer & Blair 1997). This thermal index  
290 has been valuably used to describe species or community responses to climate  
291 change. The species average lifespan calculated from (literature ? stoc capture

292 (?) is a species characteristic defining the evolutionary strategies (r/K spectrum)  
293 and the turnover rate of communities.

294

295 For each trait, we first described the temporal trends of both CWM and  
296 CWV. Then, we calculated the contribution of each species to the linear tempo-  
297 ral trend of CWM and CWV and described how these species contributions to  
298 community changes were distributed among functional and taxonomic groups.  
299 All analysis were performed using the R software environment for statistical  
300 computing and graphics and the s3cR package. The s3c (Specific Contributions  
301 to Community Changes) is a small python package written to compute com-  
302 munity weighted indices and specific contributions in their variations, while the  
303 s3cR is the R implementation of this package. Both s3c and s3cR are provided  
304 with this paper.

## 305 4.3 Results

### 306 4.3.1 Temporal Dynamics

307 The CWM of STI (also called Community Temperature Index, (Devictor *et al.*  
308 2008b)) of Mediterranean bird communities steeply decreased between 2001 and  
309 2012 with a low year to year variation (linear model:  $-0.032 \pm 0.004$  C.year,  $t=-$   
310  $6.762$ ,  $df=10$ ,  $P < 0.001$ ) (figure 2), indicating a relative enrichment of species  
311 with colder breeding ranges. This observation is coherent with other studies on  
312 Mediterranean bird communities (Gazre *et al.* 2015) using the same approach  
313 and has been related to a decrease in spring temperatures.

314

315 The CWV of STI similarly decreased over the same period (linear model:  
316  $0.049 \pm 0.008$  C.year,  $t=-5.652$ ,  $df=10$ ,  $P < 0.001$ ), indicating a relative enrich-  
317 ment of individuals characteristic of original climates compared to the other

318 species of the community. Following , the close correlation between mean and  
319 variance (Pearson's test :  $t=11.887$ ,  $df=10$ ,  $P<0.001$ ) refines the interpretation  
320 of the CWM trend, indicating that the mean variations are due to originally  
321 hot species.

322

323 The CWM of average lifespan of Mediterranean bird communities increased  
324 between 2001 and 2012 with a relatively high year to year variation (linear  
325 model:  $0.062 \pm 0.012$ ,  $t=5.119$ ,  $df=10$ ,  $P=0.001$ )(Fig. 3), meaning that commu-  
326 nities are relatively enriched with longer expected-lifespan species. The CWV  
327 of the lifespan steeply exhibits an overall weakly significant decrease (linear  
328 model:  $-0.056 \pm 0.25$ ,  $t=-2.234$ ,  $df=10$ ,  $P=0.049$ ), meaning that the community  
329 lost individuals with original lifespans over the period considered. However,  
330 the year to year variations show a sharp drop of the lifespan-based CWV be-  
331 tween 2001 and 2005, followed by a slight increase between 2005 and 2012 .  
332 Although the overall dynamics of CWM and CWV were not substantially re-  
333 lated (Pearson's test :  $t=-1.2164$ ,  $df=10$ ,  $P=0.25$ ), a visual inspection suggests  
334 a slight anti-correlation in the first years, indicating a CWM variation driven  
335 by originally short-lived species.

### 336 4.3.2 Species contributions

337 Decoupling the temporal trends of community indices between species contri-  
338 butions (Fig. 4 and 5, top) revealed that species were contributing differentially  
339 to the indices' trends, even if weak but significant correlations were observed  
340 when comparing the species contribution to each indices.

341

342 The distributions of species contributions were zero-truncated, indicating  
343 that only a few key contributor species shaped the trends in community indices.  
344 The additive properties of contributions enabled us to sum the contributions

345 by taxonomic order, the four categories of species deduced from the respective  
346 signs of their originality and the temporal trend of their relative abundances  
347 (Fig. 4 and 5, middle).

348 **STI-based CWIs** The taxonomic clustering of species contributions allowed  
349 us to compute the average species contributions of each bird order represented in  
350 the Mediterranean domain. Our results showed that four orders (Coraciiformes,  
351 Cuculiformes, Columbiformes, Passeriformes) exhibited high average species  
352 contributions, whereas others (Galliformes, Charadriiformes, Apodiformes, Ac-  
353 cipitiformes) were not contributing to the CWM and CWV dynamics. The  
354 Falconiformes were the only order substantially contributing against the CWI  
355 trends.

356

357 The functional clustering of species contributions showed that the negative  
358 trend of the STI-based CWM seemed to be mainly due to hot-dwelling species  
359 experiencing negative temporal trend. The decrease in the variance of the STI  
360 seems to be driven by both hot-dwelling species with a negative population  
361 trend (as conjectured from the cwm-cwv correlation) and cold-dwelling species  
362 with a positive population trend. When looking at the distribution of species  
363 contributions among migratory strategies, both CWM and CWV trends were  
364 clearly shaped by migratory birds.

365 **Lifespan-based CWIs** When clustered by order, the average species contri-  
366 butions of the CWM and the CWV trends showed that the same three dominant  
367 order were driving the STI and lifespan based CWI contributions. However, the  
368 Accipitriformes showed a high mean contribution to the CWV trend and only  
369 two orders (Galliformes, Charadriiformes) did not substantially contribute to  
370 the trends. Again, the Falconiformes were contributing against the global com-



371 munity trends.

372

373 The functional clustering of species contributions showed that the increase of  
374 the average community lifespan was driven by decreasing populations of short-  
375 lived species and increasing populations of long-lived species. The slight decrease  
376 of the lifespan CWV was driven by both increases and decreases of long-lived  
377 species. Again, the CWI trends were mainly due to the migratory species.

## 378 5 Discussion

379 Community Weighted Means (CWM) are simple and widespread indicators of  
380 the community functional composition. They have been used in a large range of  
381 studies across different natural systems (traits and communities) and as an indi-  
382 cator of climate change impact on biodiversity by the European Environmental  
383 Agency (Marcus Zisenis 2010). However, little work has been done to bring  
384 those indices beyond coarse-grained community descriptors (but see (Princ &  
385 Zuckerberg 2015)).

386 Our work expands the CWM analysis framework by introducing a decom-  
387 position of its variation in species contribution, linking community responses  
388 to species-specific dynamics, and a simple complementary functional diversity  
389 index (Community Weighted Variance). Overall these additions provide inval-  
390 uable new insights to interpret the aforementioned community-scale changes.

391

392 The documented community changes in French Mediterranean birds is a  
393 good illustration of this: between 2001 and 2012 a drop in temperature triggered  
394 an important decrease in the CWM of the species thermal index (hereafter  
395 called Community Thermal Index, CTI) (Gazre *et al.* 2015). However further  
396 characterization of this phenomenon remained elusive.

397 The substantial decrease of the realised thermal niche diversity, as measured  
398 by the associated Community Weighted Variance (CWV), suggests a jeopar-  
399 dization in the ability of communities to adjust their composition in response to  
400 further environmental change. Moreover, the strong correlation between com-  
401 munity weighted means and variance suggests that the change was driven by  
402 local extirpations of particularly hot-dwelling species (i.e species carrying rela-  
403 tively high and original thermal indices).

404 The decomposition of the community trend in species contributions cor-  
405 roborates those results and open a novel range of questions. By allowing the  
406 aggregation of species trends, this method showed that migratory species are  
407 on average higher contributors to the community dynamics, for both STI and  
408 lifespan traits. This result are in agreement with the hypothesis that species  
409 with larger ability to shift their distribution range are more likely to track brutal  
410 environmental changes (Jiguet *et al.* 2007; Leroux & Loreau 2008).

411 Overall this framework could be used to check the community-wide nature  
412 of perturbations and single out the species to focus on in policy conception.

413

414 The community weighted indexes (CWM and CWV) framework is a simple  
415 functional measure of a community, rooted in the interaction milieu paradigm  
416 (McGill *et al.* 2006). It offers a simple univariate alternative to encompassing  
417 multitraits methods (e.g. hypervolumes (Blonder *et al.* 2014)). This simplicity  
418 allow for more straightforward interpretation.

419 Hence, the trait selection must be careful and in line with the ecological ques-  
420 tion asked. For instance, one can distinguish *specific indicator values* (Species  
421 thermal index, Ellenberg averaged values), defined at species level, are naturally  
422 linked to environmental parameters (for instance in environmental calibration  
423 (Ter Braak, Cajo JF & Barendgret, Leo G. 1986)). Conversely *functional traits*

424 (body mass, lifespan, leaf area... (Violle *et al.* 2007)), defined at the individual  
425 level (thus allowing the measure of intraspecific variability), are naturally linked  
426 with evolutionary strategies ( $r/K$ ) and ecological performances (productivity),  
427 or ecosystem functioning (Reiss *et al.* 2009). Note that if relative abundance is  
428 itself used as a trait, the CWM is equal to Simpson's diversity index and the  
429 associated CWV is a community evenness measure (Hill 1997).

430 Overall these indices are able to carry functional information (as opposed  
431 to species richness or evenness measures) while staying focused on the traits  
432 relevant to the phenomenon studied (as opposed to more general functional di-  
433 versity measures).

434

435 Specific-contribution decompositions as we outlined them are exact only on  
436 linear trends fitted with ordinary least squares. For more complex dynamics, we  
437 advise to use contributions on well chosen linear segments of the variations, to  
438 study a particular phase of the community changes, or between two given dates  
439 to study the overall changes without concern for the intermediary fluctuations.

440 The most commonly pointed out shortcoming of CWM is not addressed here:  
441 the difficulty to disentangle effects from climate change from confounding vari-  
442 able (e.g. land use modifications contemporary of climate change that would  
443 also influence the trait value) (Clavero *et al.* 2011; Barnagaud *et al.* 2012; 2013;  
444 Davey *et al.* 2013; Roth *et al.* 2014; Zografou *et al.* 2014) Ultimately, going  
445 beyond statistical correlation to causal explanations would require the use of  
446 controlled experimentation at community scale.

447

448 Nevertheless, one of the most promising approach allowing a relevant iden-  
449 tification of land use versus climate change effect lies in the study of the spatio-  
450 temporal dynamics of diversity. Although they are tricky to disentangle over

451 large spatial or temporal extent, their local-scale temporal variations are not  
452 expected to be concomitant. This hypothesis could be relatively easily tested  
453 because our framework is still valid when comparing community through space  
454 rather than time.

455 Another promising line of questioning would use the aggregative properties of  
456 the contribution. Indeed, preliminary results in our bird dataset showed that the  
457 distribution of contributions are presenting a taxonomic structure, with some  
458 orders systematically associated with strong contributions values. A systematic  
459 study of the putative phylogenetic signal of contributions could lead to new  
460 insight on the evolutionary basis of community perturbation patterns.

## 461 6 Data accessibility

462 The following are provided with the manuscript:

- 463 • STOC data for the mediterranean region (2001-2012)
- 464 • s3c python package implementing the computation of CWI and contribu-  
465 tions.
- 466 • s3cR R package implementing the computation of CWI and contributions.
- 467 • Scripts wrote with those packages and data that were used to produces  
468 the figures

## 469 A Proofs

470 In the following section we consider a community of  $N$  individuals,  $R$  species with  
471  $p_i$  the relative abundance of species  $i$  and  $t_i$  the value of the trait of species  $i$ .

472 **A.1 Jackknife contribution equation**

473 Using the ordinary least square method, the estimation of beta is:

$$\hat{\beta} = \frac{\sum_i (t_i - \bar{t})(CWM(t_i) - \overline{CWM})}{\sum_i (t_i - \bar{t})^2} \quad (17)$$

474 Thus:

$$c_k = \beta - \beta_{i \neq k} \quad (18)$$

$$= \frac{1}{\sum_i (t_i - \bar{t})^2} \sum_i (t_i - \bar{t}) (CWM(t_i) - \overline{CWM} - CWM_{i \neq k}(t_i) + \overline{CWM}_{i \neq k}) \quad (19)$$

475 When removing a species  $k$ , its relative abundance is equally reported on all

476 other species. Hence the  $\Delta P$  is:

$$\Delta p_i = \begin{cases} -p_k & \text{if } i = k \\ \frac{p_k}{N-1} & \text{if } i \neq k \end{cases} \quad (20)$$

477 Thus, the variation of CWM is given by:

$$c_k = \frac{CWM_{i \neq k} - CWM}{1} = \Delta CWM = \theta \Delta P \quad (21)$$

$$= \sum_{i \neq k} \theta_i \frac{p_k}{N-1} - \theta_k p_k \quad (22)$$

$$= p_k \frac{\sum_{i \neq k} \theta_i}{N-1} - \theta_k \quad (23)$$

$$= p_k \overline{\theta_{i \neq k}} - \theta_k \quad (24)$$

478 Where  $\overline{\theta_{i \neq k}}$  is the average trait value of all species but  $k$ . On a more general

479 standpoint we can define a *Thermal originality* vector  $O$  so that  $o_i = \overline{\theta_{j \neq i}} - \theta_i$ .

480 Using the expression 24 in 19 :

$$c_k = \mathbb{P} \frac{1}{n_i(t_i - \bar{t})^2} \times_i^{\mathcal{R}} (t_i - \bar{t}) CWM(t_i) - \overline{CWM} - CWM(t_i) + p_k(t_i)o_k + \overline{CWM - p_k o_k} \quad (25)$$

$$= \mathbb{P} \frac{1}{n_i(t_i - \bar{t})^2} \times_i^{\mathcal{R}} (t_i - \bar{t}) [p_k(t_i)o_k - \overline{p_k o_k}] \quad (26)$$

$$= \mathbb{P} \frac{o_k}{n_i(t_i - \bar{t})^2} \times_i^{\mathcal{R}} (t_i - \bar{t}) [p_k(t_i) - \overline{p_k}] \quad (27)$$

## 481 A.2 New contribution equation

By linearity of a CWM with respect to relative proportions:

$$\begin{aligned} \Delta CWM &= \times_i^{\mathcal{R}} \theta_i \Delta p_i \\ \Delta CWM &= \overset{\text{O}}{\text{O}} \overset{1}{\text{X}} \times_{i \neq j} \theta_i \Delta p_i^A + \theta_i \Delta p_j \end{aligned}$$

482 As the sum of relative abundances is always one, we have:

$$\times_i^{\mathcal{R}} \Delta p_i = 0 \Leftrightarrow \Delta p_j = - \times_{i \neq j} \Delta p_i$$

Thus:

$$\begin{aligned} \Delta CWM &= \overset{\text{O}}{\text{O}} \overset{1}{\text{X}} \times_{i \neq j} \theta_i \Delta p_i^A - \theta_i \times_{i \neq j} \Delta p_i \\ \Delta CWM &= \times_{i \neq j} \Delta p_i (\theta_i - \theta_j) \\ \Delta CWM &= \times_i^{\mathcal{R}} \Delta p_i (\theta_i - \theta_j) \quad (\text{as } \Delta p_j (\theta_j - \theta_j) = 0.) \end{aligned}$$

483 If we sum over all possible values of  $j$  we have:

$$R\Delta CWM = \sum_{j=1}^{\mathcal{R}} \sum_{i=1}^{\mathcal{R}} \Delta p_i (\theta_i - \theta_j) \quad (28)$$

Because the sum is commutative :

$$\begin{aligned} R\Delta CWM &= \sum_{i=1}^{\mathcal{R}} \sum_{j=1}^{\mathcal{R}} \Delta p_i (\theta_i - \theta_j) \\ R\Delta CWM &= \sum_{i=1}^{\mathcal{R}} \Delta p_i \sum_{j=1}^{\mathcal{R}} (\theta_i - \theta_j) \\ \Delta CWM &= \sum_{i=1}^{\mathcal{R}} \Delta p_i \frac{1}{R} \sum_{j=1}^{\mathcal{R}} (\theta_i - \theta_j) \\ \Delta CWM &= \sum_{i=1}^{\mathcal{R}} \Delta p_i \Omega_i = \sum_{i=1}^{\mathcal{R}} C_k \end{aligned}$$

### 484 A.3 Variance decomposition

485 (We assume that  $\frac{N}{N-1}$  is constant).

$$\Delta CWV = \sum_{i=1}^{\mathcal{R}} \Delta p_i t_i^2 - \Delta(CWM^2) \quad (29)$$

486 Firstly, by analogy with the previous section, we have:

$$\sum_i \Delta p_i t_i^2 = \sum_i \Delta p_i \frac{1}{R} \sum_j t_i^2 - t_j^2 \quad (30)$$

487 We note  $\omega_i = \frac{1}{R} \sum_j t_i^2 - t_j^2$  by analogy to  $\Omega_i = \frac{1}{R} \sum_j t_i - t_j$

Secondly, we have:

$$\Delta(CWM^2) = \left[ \sum p_i^{(1)} t_i \right]^2 - \left[ \sum p_i^{(0)} t_i \right]^2 \quad (31)$$

We note:

$$\begin{aligned}
 d_i^j &= t_i - t_j \\
 \alpha_1 &= \prod_{i=1}^R p_i^{(1)} d_i^j \\
 \Delta p_i &= p_i^{(1)} - p_i^{(0)}
 \end{aligned}$$

488 As  $p_j = 1 - \prod_{i \neq j} p_i$ , we have  $\prod p_i^{(1)} t_i = \alpha_1 + t_j$ . Thus:

$$\begin{aligned}
 \Delta(CWM^2) &= [\alpha_1 + t_j]^2 - [\alpha_0 + t_j]^2 \\
 &= \alpha_1^2 + 2t_j\alpha_1 + t_j^2 - (\alpha_0^2 + 2t_j\alpha_0 + t_j^2) \\
 &= (\alpha_1 - \alpha_0) [(\alpha_1 + \alpha_0) + 2t_j] \\
 &= \left( \prod_i \Delta p_i d_i^j \right) 2t_j + \prod_k (p_k^{(1)} + p_k^{(0)}) d_k^j \\
 &= \prod_i \Delta p_i d_i^j 2t_j + \prod_k (p_k^{(1)} + p_k^{(0)}) (t_k - t_j) \\
 &= \prod_i \Delta p_i d_i^j 2t_j + \prod_k t_k (p_k^{(1)} + p_k^{(0)}) - t_j \prod_k (p_k^{(1)} + p_k^{(0)}) \\
 &= \prod_i \Delta p_i d_i^j [CTI_0 + CTI_1] \\
 &= \prod_i \Delta p_i d_i^j S
 \end{aligned}$$



If we sum over all possible values of  $j$ :

$$\begin{aligned}
 R\Delta(CWM^2) &= \sum_j \sum_i \Delta p_i d_j^i S \\
 \Delta(CWM^2) &= \frac{1}{R} S \sum_j \sum_i \Delta p_i (t_i - t_j) \\
 &= S \sum_j \Delta p_j \frac{1}{R} \sum_i (t_i - t_j) \\
 &= S \sum_i \Delta p_i \Omega_i
 \end{aligned}$$

Finally using equations 30 and ?? in 29 we have:

$$\Delta CWV = \sum_{i=1}^{\mathcal{R}} \Delta p_i (\omega_i - S\Omega_i) = \sum_{i=1}^{\mathcal{R}} \mathcal{C}_i \quad (32)$$

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Figure 1: **Variation of CMW/CWV and their interpretations.** The addition of the CWV precise the variation of the cwm.

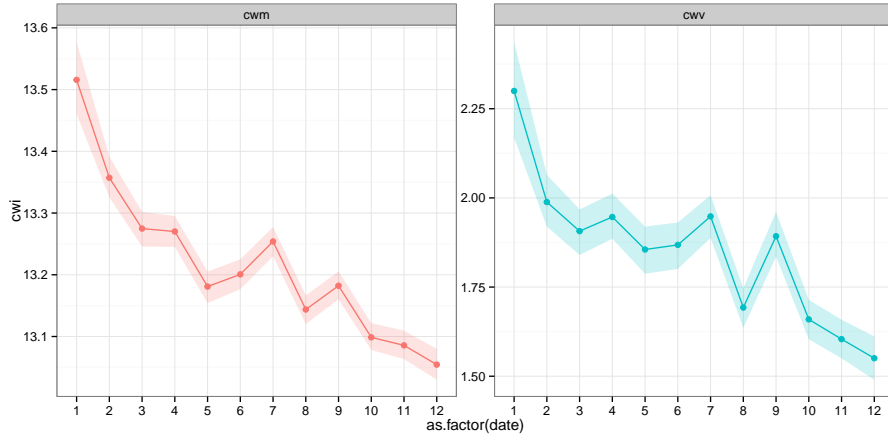


Figure 2: Annual values (2001-2012) of French Mediterranean Bird Communities Weighted Mean (left) and Variance (right) of STI. Shaded areas are 90% bootstrap confidence intervals

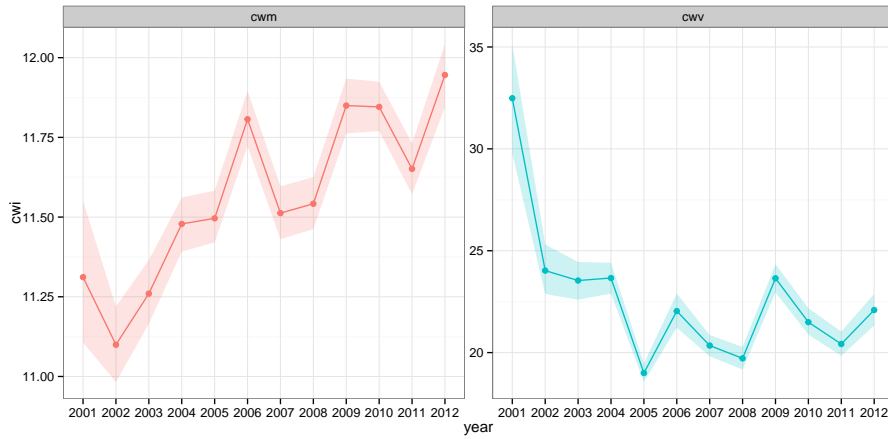


Figure 3: Annual values (2001-2012) of French Mediterranean Bird Communities Weighted Mean (left) and Variance (right) of lifespan. Shaded areas are 90% bootstrap confidence intervals

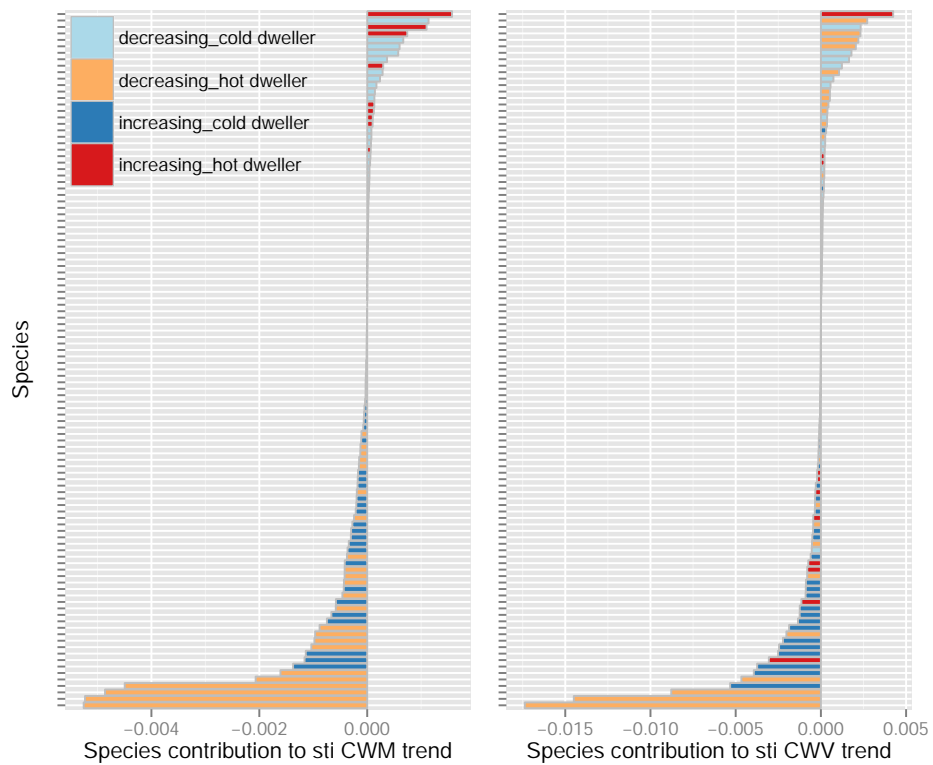


Figure 4: Species contribution of French Mediterranean Bird Communities Weighted Mean (left) and Variance (right) of STI for the period 2001-2012. Red=originally hot species with increasing population; Orange: originally hot species with decreasing population; blue=originally cold species with increasing population; skyblue: originally cold species with decreasing population.

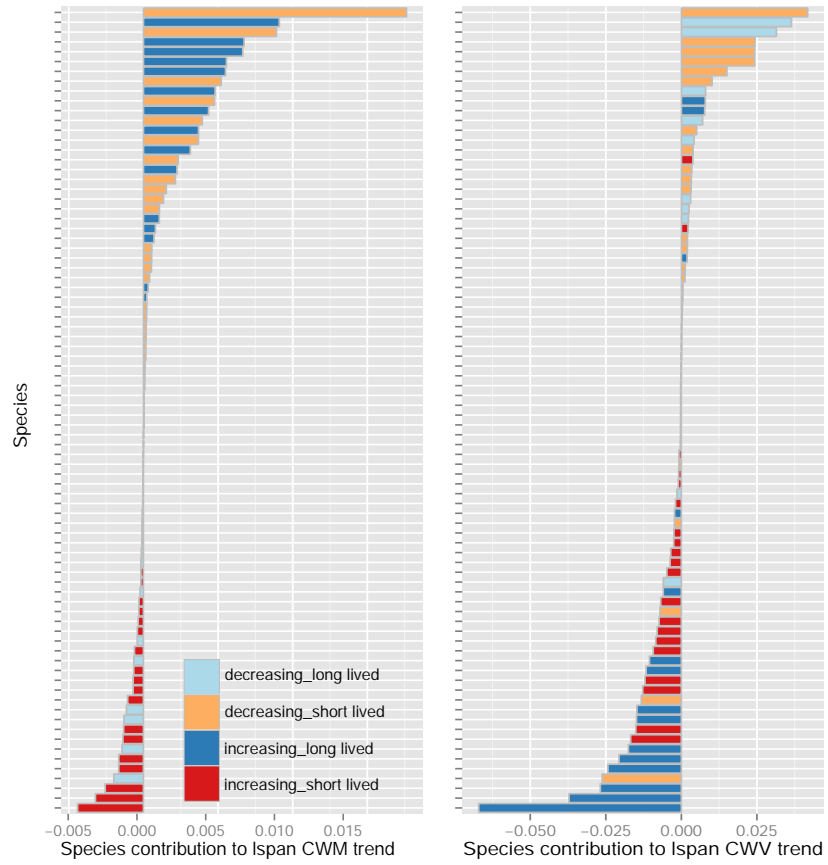


Figure 5: Species contribution of French Mediterranean Bird Communities Weighted Mean (left) and Variance (right) of lifespan for the period 2001-2012. Red=long-lived species with increasing population; Orange:long-lived species with decreasing population; blue=short-lived species with increasing population; skyblue: short-lived species with decreasing population.

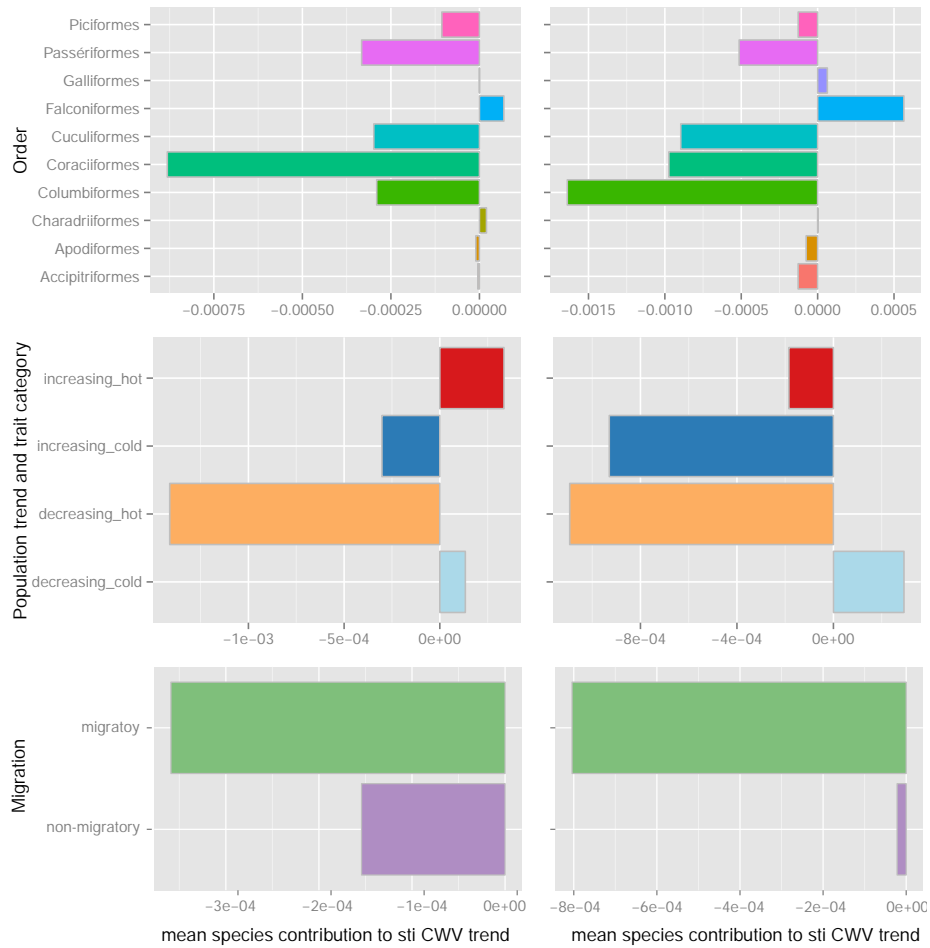


Figure 6: Mean species contributions of common birds community weighted indexes of sti in the mediterranean region of France for the period 2001-2012 Top : Mean contribution by taxonomical order. Middle: Mean contribution by sti and population trend category : Red/orange: originally long-lived species, blue/purple: originally short-lived species. Bottom: Mean contributions for migratory and non migratory birds.

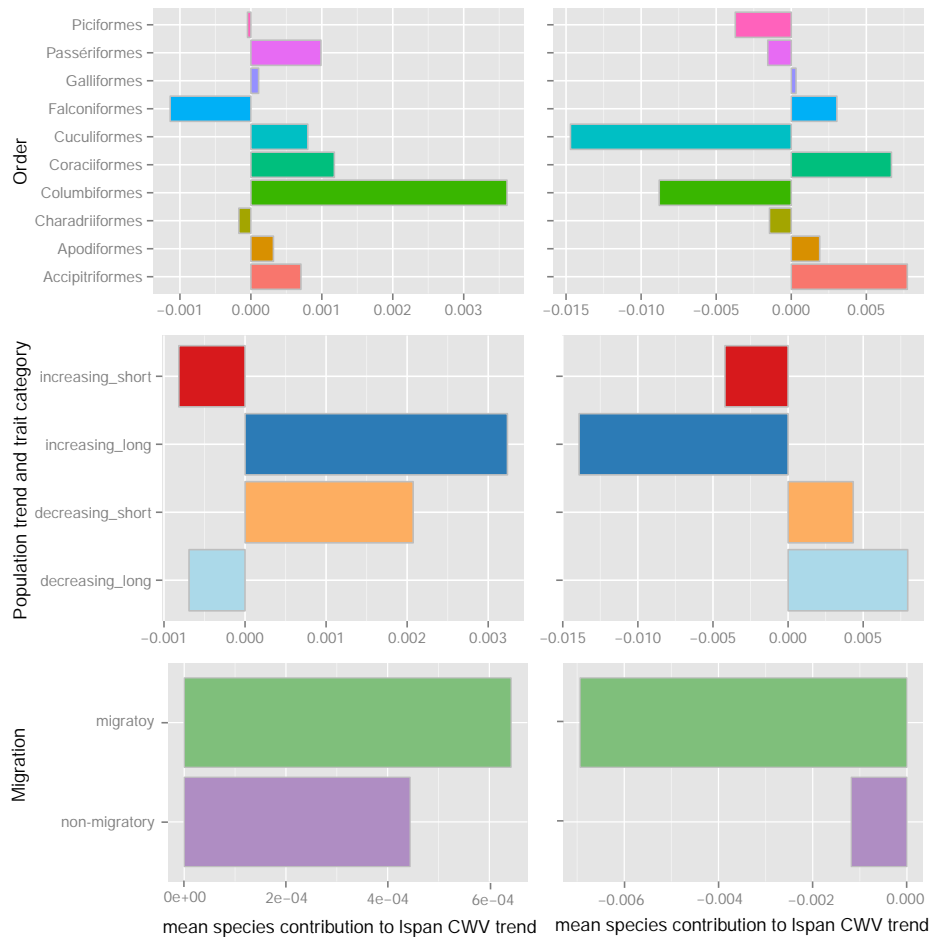


Figure 7: Mean species contribution of French Mediterranean Bird Communities Weighted Mean (left) and Variance (right) of lifespan for the period 2001-2012 Top : Mean contribution by taxonomical order. Middle: Mean contribution by sti and population trend category : Red/orange: originally long-lived species, blue/purple: originally short-lived species. Bottom: Mean contributions for migratory and non migratory birds.

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