A general framework for estimating species contribution to community changes

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May 14, 2015

Abstract

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

We apply this approach to the reshuffling of common birds communities in the French Mediterranean area between 2001 and 2012. The empirical analysis confirms that our approach helps understanding the species dynamic patterns that shape the changes at the community level and reveals
the key species responsible for directional changes in functional composition.

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

Keywords: community ecology, community weighted means, functional biogeography, niche, interaction milieu, birds, global changes.

1 Introduction

Community ecologists working on global changes have faced the dilemma of either aggregating complex information using meaningful indices (such as species richness, diversity indices or more elaborated indices of community composition) or working on single species information. A consequence of the tension between these two levels of information - community and species - is that which species contribute to explain changes in community diversity and composition, and how such contribution occurs, is often ignored. Conversely, studying individual species responses to environmental changes may not allow scaling up to community level responses, in particular because of the importance of species interactions in such responses.

The challenge of linking community changes with individual species dynamics has contributed to divide empirical and conceptual global change studies in two main branches. On the one hand, community-level approaches have schematically focused on describing spatial and temporal trends in diversity and composition in space and time. In this context, species richness or diversity
indices are often used as integrative descriptors of the community (Mackey & Currie 2001) environmental changes, community structure and composition are expected to be modified depending on community assembly rules (Logue et al. 2011). On the other hand, species-level approaches have broadly focused on how individual species occurrences or abundances are distributed along environmental gradients. Following a disturbance, species abundances and distributions are expected to be altered according to the position and breadth of the species niche. For instance, climate change is expected to trigger range shifts of many species if those species are tracking the climate according to their specific temperature preference (Thomas et al. 2004).

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

To overcome these limits, two methodological approaches have been developed that provide a description of community responses using trait rather than species - diversity. A first available approach integrating trait variability
within communities consists in defining communities functional structure as the
distribution of species and their abundances in the functional space character-
ized by multiple functional traits (Villger et al. 2008). This multidimensional
approach allows the quantification of inter-species variability in the traits con-
sidered. Therefore, two communities with similar functional richness but uneven
distribution of individuals among functional traits and/or very original traits
can be differentiated. The use of this multidimensional functional space based
on species traits has emerged as a useful way to quantify expected changes in
community structure after disturbances (Mouillot et al. 2013).

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

Although these two types approaches have clearly been useful to describe
general changes in species assemblages, they still mask species-specific dynamics. In particular, a change in functional space or CWM do not tell which species and traits have been lost or gained and whether it is driven by few key species or by the entire species pool. Moreover, integrating inter- versus intra-species variability is not explicitly considered. Overall, a simple general framework allowing to monitor changes in community and species dynamics while accounting for functional differences between and within species is missing. Yet, to shed lights on the processes responsible for observed community changes, knowing how much each individual species contributes, as well as the direction and magnitude of these contributions, might be relevant. For instance, following climate change, conservation implications would be very different if only two or three focal species are responsible for an observed change in a community-based index. Further, assessing the contributions for meaningful functional groups (e.g. protected vs unprotected, competitive or not, exotic or resident) might be of interest to test ecological predictions or to help designing conservation plans.

Here, we propose a general framework, along with open source software to perform such analyses, to assess the contributions of species or group of species to CWM variations. We then introduce the community-weighted variance (CWV) as a new functional diversity indicator and propose a way to compute species contributions to its variations. Finally, we present an application of this method to the French breeding bird survey.
2 Partition of Community Weighted Mean variations

2.1 An interaction milieu descriptor

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

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

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

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

2.2 Species contributions

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

\[
C_k = \beta_{i\neq k} - \beta
\]  

(2)

We propose a direct expression for the specific contribution \( C_k \). Because of the linear nature of the CWM with respect to the trend in relative abundance, this expression is exact if the trends are approximated by an ordinary least square regression of the index as a function of time. In this case, the contribution of species \( k \) is equal to the product of the linear trend of its relative abundance \( \Delta p_k \) times its functional originality, defined by its mean difference to trait
values of the other species in the community ($o_k = \overline{\theta_{i \neq k}} - \theta_k$, see appendix A for a demonstration):

$$C_k = \Delta p_k o_k$$

(3)

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

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

$$C^*_{k} = \Delta p_k \Omega_k$$

(4)

and we now have

$$\sum_{k=1}^{R} C^*_{k} = \Delta CWM$$

(5)

Consequently, it makes sense to define the contribution of a group of species as the sum of their species contributions. This opens the way to simple decompositions of a CWM variation according to, for instance, taxonomic or functional groups of species. As an example, if $A$ is a subset of species, we have:
Using this approach and following our example of plant size-based CWM, one could segregate the contribution of C4 plants (or other distinction). Moreover, a partition between positively and negatively contributing species would be informative, all the more so as a further partition would be possible between positive contributors that have a positively original trait value and a positive relative abundance trend and the ones that have a negatively original trait value and a negative relative abundance trend.

3 Community weighted variances

3.1 A functional diversity index

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

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

$$\sum_{k \in A} C_k^* + \sum_{k \notin A} C_k^* = \Delta CWM$$

(6)
For a given trait, the CWV is a measure of the mean squared functional originality. An increase in CWV means that the community is enriched in original individuals. Conversely, a decrease in CWV is the sign that the community experiences a loss of original individuals. Going on with our plant example, such an index would allow addressing the question of whether there is an homogenization in plant height. Note that the CWV takes into account the relative species abundances as opposed to the local inter-species trait variance that has been used in previous studies (Roth et al. 2014). As a result it gives a more accurate image of the functional diversity in highly uneven communities.

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

### 3.2 Species contributions

In analogy with what we proposed for the mean, we propose a decomposition of a CWV variation that can be used to distinguish the relative contributions
of species or groups of species to the variation in the indices (see section A for a proof. This formula is exact if we use the biased sample variance estimator or if $\frac{N}{N-1}$ is constant. We have:

$$\Delta CWV = \sum_{i=1}^{R} C_i$$

with:

$$C_i = \Delta pi [\omega_i - S\Omega_i]$$

where $S$ is the sum of the initial and final CWM, $\Delta pi$ is the relative abundance variation of species $i$, $\omega_i$ its trait originality and $\omega_i$ its "variance originality".

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

$$\omega_f = \frac{1}{R} \sum_{j=1}^{R} t_i^2 - t_j$$

$$S = CWMI_i + CWMF$$

### 3.3 Taking intra-specific variation of a trait into account

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

Firstly, the CWM will not be affected by the addition of the variance of the trait (because of the linearity of the mean). However, the CWV expression
will be different since intraspecific trait variation increases the community wide variance. If we only know the intraspecific variance, we can, as a first approximation, consider that the trait value follow a normal distribution with the same mean (\(t_i\)) and variance (\(\sigma_i^2\)). Consequently, the community distribution of the trait is a Gaussian mixture and its variance is given by (Frhwirth-Schnatter 2006):

\[
\text{Var}(t) = \left[ \sum_{i=1}^{R} p_i (\sigma_i^2 + t_i^2) \right] - CWM^2 \tag{15}
\]

For species contributions, \(\omega_i\) becomes:

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

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

4 Case study: Community reshuffling of French Mediterranean bird assemblages

4.1 Data

To investigate the informative power of the approach described in the previous sections, we applied our analysis framework to the Mediterranean avifauna monitored by the French Breeding Bird Survey (FBBS) between 2001 and 2012 (Julliard et al. 2006). The FBBS is a large scale and long term monitoring program in which volunteer skilled ornithologists count birds following a standardized protocol at the same site, year after year since 2001 (Jiguet et al. 2012). Species abundances were recorded inside 2km*2km squares whose centroids were located
within a 10km radius around a locality specified by the volunteer. To improve
the representation of the diversity of habitats countrywide (Veech et al. 2012),
squares were randomly placed within the 10km buffer. On each site, volunteers
carried out 10 point counts (5min each, separated by at least 300m) twice per
spring within three weeks around the pivotal date of May 8th to ensure the de-
tection of both early and late breeders. Counts were repeated at approximately
the same date between years (7 days) and at dawn (within 14h after sunrise)
by a unique observer. The maximum count per point for the two spring sessions
was retained as an indication of point-level species abundance. We limited our
study to sites belonging to the Mediterranean biogeographic domain because of
the substantial environmental changes which occurred in this area during the
period of study (Gazre et al. 2015).

4.2 Analysis

We applied our community analysis framework to this dataset to describe the
temporal variation and the specific contributions to the CWM and CWV of
two contrasted traits: the Species Thermal Index (STI, expressed in degree
Celsius; [(Devictor et al. 2008a;b)] and the species average lifespan. The STI is
an integrative species characteristic representing the thermal preference of each
bird species. It corresponds to the average temperature experienced by a species
across its geographic range during the breeding season. STI values were com-
puted from 0.5 by 0.5 degree temperature grids (April-July averages for the pe-
species Western Palaearctic distributions at a 0.5 degree resolution from EBCC
atlas of European breeding birds (Hagemeijer & Blair 1997). This thermal index
has been valuably used to describe species or community responses to climate
change. The species average lifespan calculated from (literature ? stoc capture
The CWV of STI similarly decreased over the same period (linear model: -0.049 + 0.008 C.year, t=-5.652, df=10, P ≤ 0.001), indicating a relative enrichment of individuals characteristic of original climates compared to the other
species of the community. Following, the close correlation between mean and variance (Pearson’s test: \( t=11.887, \text{df}=10, P<0.001 \)) refines the interpretation of the CWM trend, indicating that the mean variations are due to originally hot species.

The CWM of average lifespan of Mediterranean bird communities increased between 2001 and 2012 with a relatively high year to year variation (linear model: \( 0.062 \pm 0.012, t=5.119, \text{df}=10, P<0.001 \)), meaning that communities are relatively enriched with longer expected-lifespan species. The CWV of the lifespan steeply exhibits an overall weakly significant decrease (linear model: \( -0.056 \pm 0.25, t=-2.234, \text{df}=10, P=0.049 \)), meaning that the community lost individuals with original lifespans over the period considered. However, the year to year variations show a sharp drop of the lifespan-based CWV between 2001 and 2005, followed by a slight increase between 2005 and 2012. Although the overall dynamics of CWM and CWV were not substantially related (Pearson’s test: \( t=-1.2164, \text{df}=10, P=0.25 \)), a visual inspection suggests a slight anti-correlation in the first years, indicating a CWM variation driven by originally short-lived species.

### 4.3.2 Species contributions

Decoupling the temporal trends of community indices between species contributions (Fig. 4 and 5, top) revealed that species were contributing differentially to the indices’ trends, even if weak but significant correlations were observed when comparing the species contribution to each indices.

The distributions of species contributions were zero-truncated, indicating that only a few key contributor species shaped the trends in community indices. The additive properties of contributions enabled us to sum the contributions
by taxonomic order, the four categories of species deduced from the respective
signs of their originality and the temporal trend of their relative abundances
(Fig. 4 and 5, middle).

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

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

**Lifespan-based CWIs**  When clustered by order, the average species contri-
butions of the CWM and the CWV trends showed that the same three dominant
order were driving the STI and lifespan based CWI contributions. However, the
Accipitriformes showed a high mean contribution to the CWV trend and only
two orders (Galliformes, Charadriiformes) did not substantially contribute to
the trends. Again, the Falconiformes were contributing against the global com-
The functional clustering of species contributions showed that the increase of the average community lifespan was driven by decreasing populations of short-lived species and increasing populations of long-lived species. The slight decrease of the lifespan CWV was driven by both increases and decreases of long-lived species. Again, the CWI trends were mainly due to the migratory species.

5 Discussion

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

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

The documented community changes in French Mediterranean birds is a good illustration of this: between 2001 and 2012 a drop in temperature triggered an important decrease in the CWM of the species thermal index (hereafter called Community Thermal Index, CTI) (Gazre et al. 2015). However further characterization of this phenomenon remained elusive.
The substantial decrease of the realised thermal niche diversity, as measured by the associated Community Weighted Variance (CWV), suggests a jeopardization in the ability of communities to adjust their composition in response to further environmental change. Moreover, the strong correlation between community weighted means and variance suggests that the change was driven by local extirpations of particularly hot-dwelling species (i.e. species carrying relatively high and original thermal indices).

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

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

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

Hence, the trait selection must be careful and in line with the ecological question asked. For instance, one can distinguish specific indicator values (Species thermal index, Ellenberg averaged values), defined at species level, are naturally linked to environmental parameters (for instance in environmental calibration (Ter Braak, Cajo JF & Barendgret, Leo G. 1986)). Conversely functional traits
(body mass, lifespan, leaf area... (Violle et al. 2007)), defined at the individual level (thus allowing the measure of intraspecific variability), are naturally linked with evolutionary strategies (r/K) and ecological performances (productivity), or ecosystem functioning (Reiss et al. 2009). Note that if relative abundance is itself used as a trait, the CWM is equal to Simpson’s diversity index and the associated CWV is a community evenness measure (Hill 1997).

Overall these indices are able to carry functional information (as opposed to species richness or evenness measures) while staying focused on the traits relevant to the phenomenon studied (as opposed to more general functional diversity measures).

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

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

Nevertheless, one of the most promising approach allowing a relevant identification of land use versus climate change effect lies in the study of the spatio-temporal dynamics of diversity. Although they are tricky to disentangle over
large spatial or temporal extent, their local-scale temporal variations are not
expected to be concomitant. This hypothesis could be relatively easily tested
because our framework is still valid when comparing community through space
rather than time.

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

6 Data accessibility

The following are provided with the manuscript:

- STOC data for the mediterranean region (2001-2012)
- s3c python package implementing the computation of CWI and contributions.
- s3cR R package implementing the computation of CWI and contributions.
- Scripts wrote with those packages and data that were used to produces
  the figures

A Proofs

In the following section we consider a community of $N$ individuals, $R$ species with
$p_i$ the relative abundance of species $i$ and $t_i$ the value of the trait of species $i$. 
A.1 Jacknife contribution equation

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

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

Thus:

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

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

When removing a species $k$, its relative abundance is equally reported on all other species. Hence the $\Delta P$ is:

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

Thus, the variation of CWM is given by:

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

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

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

$$= p_k (\bar{\theta}_{i \neq k} - \theta_k)$$ (24)

Where $\bar{\theta}_{i \neq k}$ is the average trait value of all species but $k$. On a more general
standpoint we can define a *Thermal orginality* vector $O$ so that $o_i = \overline{\theta_{j \neq i}} - \theta_i$.

Using the expression 24 in 19:

$$c_k = \frac{1}{\sum_i (t_i - \overline{t})^2} \sum_i (t_i - \overline{t}) \left[ CWM(t_i) - \overline{CWM} - CWM(t_i) + p_k(t_i) o_k + \overline{CWM} - p_k o_k \right]$$

(25)

$$= \frac{1}{\sum_i (t_i - \overline{t})^2} \sum_i (t_i - \overline{t}) \left[ p_k(t_i) o_k - \overline{p_k o_k} \right]$$

(26)

$$= \frac{o_k}{\sum_i (t_i - \overline{t})^2} \sum_i (t_i - \overline{t}) \left[ p_k(t_i) - \overline{p_k} \right]$$

(27)

### A.2 New contribution equation

By linearity of a CWM with respect to relative proportions:

$$\Delta CWM = \sum_{i=1}^R \theta_i \Delta p_i$$

$$\Delta CWM = \left( \sum_{i \neq j} \theta_i \Delta p_i \right) + \theta_i \Delta p_j$$

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

$$\sum_i^R \Delta p_i = 0 \iff \Delta p_j = -\sum_{i \neq j} \Delta p_i$$

Thus:

$$\Delta CWM = \left( \sum_{i \neq j} \theta_i \Delta p_i \right) - \theta_i \sum_{i \neq j} \Delta p_i$$

$$\Delta CWM = \sum_{i \neq j} \Delta p_i (\theta_i - \theta_j)$$

$$\Delta CWM = \sum_i^R \Delta p_i (\theta_i - \theta_j)$$

(as $\Delta p_j (\theta_j - \theta_j) = 0$.)

22
If we sum over all possible values of $j$ we have:

$$R\Delta CW M = \sum_{j=1}^{R} \Delta p_i (\theta_i - \theta_j)$$

(28)

Because the sum is commutative:

$$R\Delta CW M = \sum_{i=1}^{R} \sum_{j=1}^{R} \Delta p_i (\theta_i - \theta_j)$$

$$R\Delta CW M = \sum_{i=1}^{R} \Delta p_i \sum_{j=1}^{R} (\theta_i - \theta_j)$$

$$\Delta CW M = \sum_{i=1}^{R} \Delta p_i \frac{1}{R} \sum_{j=1}^{R} (\theta_i - \theta_j)$$

$$\Delta CW M = \sum_{i=1}^{R} \Delta p_i \Omega_i = \sum_{i=1}^{R} C_k$$

A.3 Variance decomposition

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

$$\Delta CWV = \sum_{i=1}^{R} \Delta p_i t_i^2 - \Delta (CW M^2)$$

(29)

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

$$\sum_{i}^{R} \Delta p_i t_i^2 = \sum_{i}^{R} \Delta p_i \frac{1}{R} \sum_{j}^{R} t_i^2 - t_j^2$$

(30)

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

Secondly, we have:

$$\Delta (CW M^2) = [\sum p_i^{(1)} t_i]^2 - [\sum p_i^{(0)} t_i]^2$$

(31)
We note:

\[ d_i^j = t_i - t_j \]
\[ \alpha_1 = \sum_{i=1}^{R_i} p_i^{(1)} d_i^j \]
\[ \Delta p_i = p_i^{(1)} - p_i^{(0)} \]

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

\[ \Delta(CWM^2) = [\alpha_1 + t_j] - [\alpha_0 + t_j]^2 \]
\[ = \alpha_1^2 + 2t_j \alpha_1 + t_j^2 - (\alpha_0^2 + 2t_j \alpha_0 + t_j^2) \]
\[ = (\alpha_1 - \alpha_0)(\alpha_1 + \alpha_0 + 2t_j) \]
\[ = \sum_i \Delta p_i d_i^j \left[ 2t_j + \sum_k (p_k^{(1)} + p_k^{(0)}) d_i^j \right] \]
\[ = \sum_i \Delta p_i d_i^j \left[ 2t_j + \sum_k (p_k^{(1)} + p_k^{(0)}) t_k - t_j \sum_k (p_k^{(1)} + p_k^{(0)}) \right] \]
\[ = \sum_i \Delta p_i d_i^j [CTI_0 + CTI_1] \]
\[ = \sum_i \Delta p_i d_i^j S \]
If we sum over all possible values of $j$:

$$R \Delta(CWM^2) = \sum_j \sum_i \Delta p_i d_i S$$

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

$$= S \sum_i \Delta p_i \frac{1}{R} \sum_j (t_i - t_j)$$

$$= S \sum_i \Delta p_i \Omega_i$$

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

$$\Delta CWV = \sum_{i=1}^{R} \Delta p_i \left( \omega_i - S \Omega_i \right) = \sum_{i=1}^{R} C_i$$ \hspace{1cm} (32)$$

References


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.


