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Decomposing changes in phylogenetic and functional diversity over space and time

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Summary

1. The α , β , γ diversity decomposition methodology is commonly used to investigate changes in diversity over space or time but rarely conjointly. However, with the ever-increasing availability of large-scale biodiversity monitoring data, there is a need for a sound methodology capable of simultaneously accounting for spatial and temporal changes in diversity.
2. Using the properties of Chao's index, we adapted Rao's framework of diversity decomposition between orthogonal dimensions to a multiplicative α , β , γ decomposition of functional or phylogenetic diversity over space and time, thereby combining their respective properties. We also developed guidelines for interpreting both temporal and spatial β -diversities and their interaction.
3. We characterised the range of β -diversity estimates and their relationship to the nested decomposition of diversity. Using simulations, we empirically demonstrated that temporal and spatial β -diversities are independent from each other and from α and γ -diversities when the study design is balanced, but not otherwise. Furthermore, we showed that the interaction term between the temporal and the spatial β -diversities lacked such properties.

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Data accessibility The site-by-species matrices and the functional tree of french avifauna are available online on the Dryad website. DOI:10.5061/dryad.93n5r

Supporting information Additional supporting information may be found in the online version of this article.

Appendix S1. Minimum and maximum value of nested β -diversities.

Appendix S2. Minimal and maximal value of β_{ST} .

Appendix S3. Simulation procedures.

Appendix S4. Details of the construction of the bird functional tree.

Appendix S5. Comments on the multivariate analysis of the spatio-temporal changes of bird functional assemblages.

Table S1. Notations for Appendix S1 and Appendix S2.

Figure S1. Pairwise scatterplot of the value of γ , β_T , β_S , β_{ST} and α obtained from a "bottom-up" simulation procedure. T was equal to 4 and S to 10.

Figure S2. Position of sites and species in the multivariate space defined by the *dpcoa*.

4. We illustrated our methodology with a case study of the spatio-temporal dynamics of functional diversity in bird assemblages in four regions of France. Based on these data, our method makes it possible to discriminate between regions experiencing different diversity changes in time. Our methodology may therefore be valuable for comparing diversity changes over space and time using large-scale datasets of repeated surveys.

Keywords

β -diversity; biodiversity; phylogenetic entropy; Shannon entropy; Hill numbers; diversity partitioning; bird assemblages; large-scale monitoring; turn-over

Introduction

Patterns of species diversity, as determined by their functional traits and phylogenetic relationships, have become central to addressing a large range of research questions such as the inference of assembly rules in community ecology (Diamond 1975; Webb 2000, Mouquet *et al.* 2012), or the delimitation of biodiversity hotspots in macro-ecology (Mazel *et al.* 2014). Using functional and phylogenetic diversity indices implicitly rejects the assumption that species are equally distinct entities, and instead accounts for their functional similarities and shared evolutionary history (Mouquet *et al.* 2012; Violle *et al.* 2007).

Thanks to the extension of large-scale biodiversity monitoring (Pereira & Cooper 2006) and the development of citizen science (Bonney *et al.* 2009), large datasets have been made available for investigating the spatial and temporal dynamics of biodiversity (Dornelas *et al.* 2014). These are of prime importance in evaluating how species assemblages are responding to on-going changes in climate and land uses. Since these temporal changes are not necessarily homogeneous across space, a depiction of biodiversity changes from both a spatial and temporal perspective (Magurran *et al.* 2010) is required to understand which processes contribute to biodiversity dynamics. An adequate methodology is therefore needed to produce meaningful measures of diversity changes over space and time.

In his seminal paper, Whittaker (1960) proposed breaking the regional species diversity (γ -diversity) down into the average within-community species diversity (α -diversity) and the between community species diversity (β -diversity). More specifically, Whittaker formulated two laws to link α , β and γ -diversities: an additive law ($\gamma = \alpha + \beta$) and a multiplicative law ($\gamma = \alpha \times \beta$). Two decomposition frameworks emerged from these two alternative approaches, each with different properties and drawbacks.

The additive law was adapted by Rao (1986) to the “Quadratic Entropy” index which generalised the Gini-Simpson index to include species dissimilarities such as functional or phylogenetic distances. He further proposed decomposing γ -diversity into several dimensions (e.g. space and time), a procedure called *Anodiv* (Pavoine 2012). However; the additive decomposition of the γ -diversity, and by extension the *Anodiv* procedure, has been criticised for its inability to produce β -diversity estimates independent from the γ - and α -diversities (Jost 2007; Baselga 2010). This property impedes *Anodiv*'s ability to access temporal or spatial biodiversity changes on large spatial scales. Indeed, large-scale

biodiversity monitoring typically covers numerous regions with variable γ and α -diversities (e.g. Devictor *et al.* 2010), a consequence of the large-scale environmental filtering and historical contingencies that shape the biogeographic gradients of diversity (Hawkins *et al.* 2003). Should β -diversities be compared across regions, it is vital that they only quantify spatial or temporal change within these regions, independently from changes in γ and α -diversities. Otherwise these two effects would become indistinguishable.

The second framework, based on Whittaker's multiplicative law, addresses this issue of independence. When diversity is calculated from an equivalent number (Hill 1973), it produces estimates of β -diversity which are independent from the α and γ -diversities (Jost 2007; Tuomisto 2010). Furthermore, the estimate of the β -diversity is set between 1 and the number of communities in the region studied. This property makes it possible to produce standardised estimates of β -diversity which are not dependent on the study design used in the region (Chao *et al.* 2012). This is a particularly important feature since large-scale biodiversity monitoring systems tend to be spatially unbalanced (Ficetola *et al.* 2013). However, despite these properties, Whittaker's multiplicative law was never adapted to breaking functional or phylogenetic diversity down into different dimensions.

We have built on these two frameworks and their respective advantages to propose a novel methodology for decomposing phylogenetic and functional diversity over space and time, and obtaining measurements of β -diversity which are independent of γ -diversity and α -diversity. This paper first introduces our multiplicative framework for estimating spatial and temporal beta diversities. Secondly, using a simulation-based approach, we demonstrate that, in the case of taxonomic diversity, the estimated β -diversities are pairwise independent from the γ and α -diversity and from each other. Finally, we illustrate its novelty and features in a case study by decomposing the spatio-temporal effects on the functional diversity of the common avifauna in four regions of France over the last decade.

Decomposing diversity over space and time

Definitions

We considered a region containing S sites in which species were recorded at T dates. We defined a community as the species composition of site s at a given date t . We defined a site pool as the pool of all communities at site s pooled for all dates, a time pool as the pool of all communities at a given date t pooled for all sites and the regional pool as the pool of all communities for all sites and dates. The spatio-temporal decomposition of diversity (multiplicative α , β , γ decomposition) will ultimately be calculated based on the ratios of the diversities in these different units (communities and pools).

Diversity index

To calculate the diversity of a given unit, we used Shannon entropy exponential. This index is an "equivalent number", part of the family of Hill numbers (Hill 1973). As such, its value ranges from 1 (if one species makes up most of the total abundance in the unit) to the number of species in the unit (if their relative abundances are all equal). It can be interpreted as the number of "equally-abundant virtual species" in the unit (Tuomisto 2010):

$$D(P) = \exp\left(-\sum_{i=1}^N \log(p_i) \times p_i\right) \quad (\text{Equation 1})$$

With P , the vector $\{p_1, p_2, \dots, p_N\}$ of abundances of the N species present in the unit studied.

To include functional and phylogenetic similarities between species, we used the version of this index formulated by Chao *et al.* (2010) from Allen's phylogenetic entropy (2009).

$$D(P) = \exp\left(-\sum_b \frac{L(b)}{T} \log(p_B(b)) \times p_B(b)\right) \quad (\text{Equation 2})$$

where the summation is made over all branches of an ultrametric phylogenetic or functional tree of tips-to-root distance T , $L(b)$ is the length of branch b , and p_B denotes the vector containing for each branch b , the summed relative abundance of its descendent species. We will refer to this index as Chao's index.

Since the index includes species similarities, its absolute value can be interpreted as the number of "equally-abundant and fully distinct virtual species" in the study unit.

Spatio-temporal decomposition

We drew inspiration from the *Anodiv* procedure (Rao 1986; Pavoine 2012) to decompose diversity according to two orthogonal factors, here time and space, according to a multiplicative framework using Chao's index. It is expressed as follows:

$$\begin{aligned} D(P_{..}) &= \frac{D(P_{..})}{\exp\left[\sum_{t=1}^T \omega_t \times \log(D(P_{.t}))\right]} \\ &\times \frac{D(P_{..})}{\exp\left[\sum_{s=1}^S \omega_s \times \log(D(P_{s.}))\right]} \\ &\times \frac{\exp\left[\sum_{t=1}^T \omega_t \times \log(D(P_{.t}))\right] \times \exp\left[\sum_{s=1}^S \omega_s \times \log(D(P_{s.}))\right]}{D(P_{..}) \times \exp\left[\sum_{t=1}^T \sum_{s=1}^S \omega_{st} \log(D(P_{st}))\right]} \quad (\text{Equation 3}) \\ &\times \exp\left[\sum_{t=1}^T \sum_{s=1}^S \omega_{st} \log(D(P_{st}))\right] \end{aligned}$$

P_{st} is the vector of species relative abundance in community at site s and date t . The formulation includes ω_{st} , a weight attributed to a community at site s and time t , that sums to 1 over all s and t based for instance on total abundance or species richness in the community. A perfectly balanced design will involve the absence of missing data and the

equal weighting of all communities, i.e. for all s and t , $\omega_{st} = \frac{1}{ST}$. Unequal weighting is not compulsory but is typically relevant when communities have been sampled with different sampling efforts (for a discussion, see Hardy & Jost 2008).

ω_s and ω_t are the weights of site pools s and time pools t , respectively, and are calculated as the sum of the weights of their constituent communities. The vector of species relative abundance for the site pool s and time pool t are thus calculated as the weighted mean of the

species relative abundances in their constituent communities: $P_{.t} = \frac{1}{\omega_t} \sum_{s=1}^S \omega_{st} P_{st}$ and

$P_{s.} = \frac{1}{\omega_s} \sum_{t=1}^T \omega_{st} P_{st}$. Finally, the vector of species relative abundances in the species pool is calculated as the weighted mean of species relative abundance across all communities:

$$P_{..} = \sum_{s=1}^S \sum_{t=1}^T \omega_{st} P_{st}$$

Equation 3 can be reformulated as:

$$\gamma = \frac{\gamma}{\alpha_T} \times \frac{\gamma}{\alpha_S} \times \frac{\alpha_S \times \alpha_T}{\gamma \times \alpha} \times \alpha \quad (\text{Equation 4})$$

With γ being the γ -diversity of the study region; with α_T and α_S being respectively the mean α -diversity of time and site pools and α the mean α -diversity of the communities in the study region. Or more simply,

$$\gamma = \beta_T \times \beta_S \times \beta_{ST} \quad (\text{Equation 5})$$

With β_T being the temporal β -diversity, β_S the spatial β -diversity and β_{ST} the interaction term between the temporal and the spatial β -diversities. If the spatial and temporal structure of the dataset is ignored, the total β -diversity β of the region across time can be expressed as:

$$\beta = \frac{\gamma}{\alpha} = \beta_T \times \beta_S \times \beta_{ST} \quad (\text{Equation 6})$$

Properties of the β -diversities—Chiu *et al.* (2014) demonstrated that Chao's index obeyed the “replication principle”. This implies that β_T and β_S have several of the properties enumerated in Jost (2007) and Tuomisto (2010), which facilitate the interpretation of their numerical values:

- β_T and β_S are pairwise independent from γ , and from α_T and α_S , respectively (Jost 2007; Baselga 2010). Using simulations, we demonstrate below that β_T and β_S are pairwise independent from each other and are both pairwise independent from α .
- The values of β_S (resp. β_T) are intuitive and can be interpreted as “the number of virtual, fully dissimilar, and equally abundant site pools (resp. time pools)” in the study region.
- The values of β_S , β_T and β have a range that is only dependent on the weights of respectively the site pools, time pools and the communities:

$$\begin{aligned}
 1 \leq \beta_T \leq N_T, \text{ with } N_T &= \exp \left[- \sum_{t=1}^T \omega_t \times \log(\omega_t) \right] \\
 1 \leq \beta_S \leq N_S, \text{ with } N_S &= \exp \left[- \sum_{s=1}^S \omega_s \times \log(\omega_s) \right] \\
 1 \leq \beta \leq N_{ST} \text{ with } N_{ST} &= \exp \left[- \sum_{t=1}^T \sum_{s=1}^S \omega_{st} \times \log(\omega_{st}) \right]
 \end{aligned}$$

The minimum possible value of β_S , β_T and β will be 1 if the site pools, time pools or communities respectively are identical. The maximum possible value of β_S , β_T and β will be attained if the site pools, time pools or communities respectively do not share species or tree branches. N_S , N_T and N_{ST} can be interpreted as the equivalent number of sites pools, times pools and communities, respectively. If all communities are weighted equally, they will be equal to S , T and ST , respectively.

In other words, our measurement of change in diversity over space (resp. over time) has a natural minimum and maximum. Thus the absolute values of β_S and β_T can be standardised by their minimum and maximum value to make their value independent from the number of

sites and time periods studied (Chao et al. 2012): $Std_{\beta_S} = \frac{\beta_S - 1}{N_S - 1}$ and $Std_{\beta_T} = \frac{\beta_T - 1}{N_T - 1}$

– β_{ST} has a minimum value of 1 and a maximum value constrained by both the value of β_S and β_T (see Appendix S2 for the demonstration),

$$1 \leq \beta_{ST} \leq \min \left(\frac{N_{ST}}{N_S} \times \frac{1}{\beta_T}, \frac{N_{ST}}{N_T} \times \frac{1}{\beta_S} \right).$$

Relationship to the nested decomposition of diversity—Another methodological choice that can be made when analysing a spatio-temporal dataset is to consider that space and time are nested (e.g. Sobek *et al.* 2009). If space is considered as nested within time periods, a new measure $\beta_{S/T}$ can be formulated to characterise the mean spatial β -diversity of the region within time periods (Pavoine & Dolédec 2005; Tuomisto 2010).

The decomposition will then be expressed as:

$$\gamma = \beta_T \times \beta_{S/T} \times \alpha \quad (\text{Equation 7})$$

meaning that $\beta_{S/T} = \frac{\alpha_T}{\alpha} = \beta_S \times \beta_{ST}$. Alternatively, if we consider time periods as nested within space:

$$\gamma = \beta_S \times \beta_{T/S} \times \alpha \quad (\text{Equation 8})$$

meaning that $\beta_{S/T} = \frac{\alpha_S}{\alpha} = \beta_T \times \beta_{ST}$.

Thus, $\beta_{S/T}$ and $\beta_{T/S}$ are not strictly β -diversities because they are the ratio of two mean α -diversities from different hierarchical levels, rather than the ratio of a unit's diversity and the diversity of its subunits. However, we demonstrated (Appendix S1) that like β -diversities, they have fixed minimum and maximum values that are independent of the γ and α -

$$\text{diversities: } 1 \leq \beta_{S/T} \leq \frac{N_{ST}}{N_T} \text{ and } 1 \leq \beta_{T/S} \leq \frac{N_{ST}}{N_S}.$$

Interpretation of β -diversities

The different β -diversities can be interpreted on their own and in combination with each other (Figure 1). β_T quantifies the change in diversity between time pools, or in other words, the temporal change in regional diversity, irrespective of the spatial patterns of diversity. β_S quantifies the change in diversity between site pools, or in other words, the spatial change in diversity after averaging the temporal variability of communities. β_{ST} quantifies the interaction between spatial and temporal turnover, it can be used to quantify finer changes such as a rearrangement of species between sites between two dates which are not quantified by β_S and β_T (Figure 1). The case where β_{ST} is equal to 1 indicates that there is an identical change of diversity across space and time between communities; for instance, if between two dates a species is introduced in all studied communities at equal relative abundance. On the other hand, a value of β_{ST} over 1 denotes a heterogeneity of change of communities over space and time that is not quantified by β_S and β_T because it averages out at larger spatial or temporal scales. It is interesting to note that it is possible to have a situation where β_S and β_T equal one while β_{ST} is higher than one. This is illustrated in Figure 1 ($\beta_S = \beta_T = 1$ and $\beta_{ST} > 1$) with an extreme case in which two communities fully inverted their composition between the two dates studied. A concrete example could be the mosaic theory of forest regeneration (Remmert 1991): disturbances in a forested landscape would trigger the same temporal successions but at different times and locations generating a heterogeneous landscape. In this case, there is a spatial and temporal change between communities, but the time pools remain constant (in other words, the diversity of the region changes very little between the two dates) and the site pools also remain constant (in other words, when averaged over time, communities across the landscape have a similar composition).

Test of functional and phylogenetic β -diversities

A common way to test the values of functional or phylogenetic β -diversities is to use a randomisation model to generate a distribution of β -diversities under a certain null hypothesis. Our framework is compatible with any kind of randomisation procedure. In the following case study of French avifauna, we chose the species shuffling procedure that has been shown to be among the most efficient null models in terms of Type I error rate (Hardy 2008). A significant high (resp. low) β -diversity thus indicates that species tend to be replaced by dissimilar (resp. similar) species over time or space. We calculated the effect size of each functional β -diversity, as the observed β -diversity minus the mean of its null distribution divided by the standard deviation of the null distribution. If the β -diversity was higher than expected (positive effect size) then the communities differed more than expected under a random assembly model; if the β -diversity was lower than expected (negative effect size), then the communities differed less than expected under a random assembly model.

Independence properties of the spatio-temporal diversity decomposition

We adapted the simulation procedures developed by Baselga (2010) to demonstrate the independence properties of our diversity decomposition framework. We used two simulation approaches: 1) a top-down approach where we first chose a γ value then generated a community weight vector and sequentially randomly selected the values of α_T , α_S and α ; 2) a bottom-up approach where we first chose an α value, then generated a community weight vector and sequentially randomly selected the values of α_T , α_S and γ . Each draw was constrained by minimum and maximal values deduced from the properties of the spatio-temporal decomposition stated above. For a given number of sites (S) and dates (T), we tested 200 initial γ or α values between 1 and 200, each repeated 200 times. Both the top-down and bottom-up approach procedures are detailed in Appendix S3. Both procedures are necessary to demonstrate the pairwise independence of the β -diversities from γ and α (Baselga 2010). In the top-down approach, the β -diversities need to be uncorrelated with γ and in the bottom-up approach, the β -diversities need to be uncorrelated with α .

When no data were missing (i.e. all sites observed at all times) and $T=4$ and $S=10$, we found no correlation of γ with $\text{Std}\beta_T$ (Figure 2, $r = 0.0039$; 95% CI interval: $[-0.0059, 0.014]$), γ with $\text{Std}\beta_S$ (Figure 2, $r = -0.00027$; 95% CI interval: $[-0.010, 0.0095]$) or $\text{Std}\beta_T$ with $\text{Std}\beta_S$ (Figure 2, $r = 0.02$; 95% CI interval: $[-0.013, 0.0069]$) in the top-down approach and no correlation of α with $\text{Std}\beta_T$ or α with $\text{Std}\beta_S$ in the bottom-up approach (Figure S1. α and $\text{Std}\beta_T$: $r = 0.0052$; 95% CI interval: $[-0.0046, 0.015]$). In contrast, β_{ST} depended on the previously established β_T and β_S values, but is independent from both γ and α (Figure 2. β_{ST} and γ : $r = 0.00038$; 95% CI interval: $[-0.0094, 0.010]$. Figure S1. β_{ST} and α : $r = 0.0037$; 95% CI interval: $[-0.0061, 0.0135]$). When we further explored alternative T and S parametrizations (for any values of S and T between 2 and 10), we found these results to be robust (Table 1).

We also investigated the specific case where community data were missing in the dataset. For all T and S parameter values, a varying proportion of community weights were set to 0 while maintaining at least one community per site and date. We then studied how the amount of missing data affects the independence properties between γ , β_T , β_S , β_{ST} and α . We found that in the extreme case of perfect balance (all community weights are equal), all correlations remained close to 0. When we introduced unequal weighting and increased the proportion of missing data, the correlation between β_T and β_S increased slightly but remained on average close to 0. However there were some extreme correlation values that deviated strongly from 0. We observed the same pattern for the other relationships although they tended to show more robustness (Figure 3). This can be explained by the fact that the sampling design becomes less orthogonal between sites and dates as the amount of missing data increases. The extreme case would be a spatial-temporal dataset where a single community was sampled per date, each time at different locations. Then β_T and β_S would be equal. However, as indicated by the correlation values, which were on average close to 0, the independence relationship remained on average quite robust and only a few weight vectors resulted in a loss of the independence properties.

Overall we therefore conclude that β_T , β_S and β_{ST} are pairwise independent from α and γ . We further conclude that β_T and β_S are pairwise independent from each other but only when the weighting scheme does not deviate too far from a perfectly balanced sampling design

(i.e. no missing data and for all s and t , $\omega_{st} = \frac{1}{ST}$).

Our simulation procedure has its limitations. Indeed, it is not clear how the inclusion of a phylogenetic or functional tree between species could further constrain the distribution of the different diversity metrics compared to the maximal values of β_T , β_S and β_{ST} previously fixed. It is however intuitive that the maximum number of completely distinct communities, site pools or time pools is equal to the number of functional/phylogenetic tree branches that emerge from the root. Therefore although our simulation procedure concurs with the current understanding of the diversity decomposition using Chao's index, it should be specified that our approach is more strictly appropriate for borderline cases where species are fully distinct or when the inclusion of a functional or phylogenetic tree does not affect the potential distribution of the diversity measures. In other cases, it is possible that the independence properties we empirically accessed would be altered.

Case study: spatio-temporal changes in functional diversity in French bird assemblages

Data

We applied our spatio-temporal framework to the avifauna monitored by the French breeding bird survey programme (Julliard *et al.* 2006). This programme relied on skilled ornithologists to monitor common birds using a standardised protocol from 2001 to 2012. Under this scheme, ornithologists recorded every individual seen or heard during a five-minute period at 10 count points, evenly distributed within 2×2 km survey sites. The sites were randomly selected around the observer's locality, thus ensuring that a variety of habitats were monitored (including intensive farmlands, forests, suburbs and cities). We selected four regions, each defined as a circular window 100 km in diameter, belonging to two disparate biogeographic regions. Two were situated on the Mediterranean coast (MED1 and MED2) and two on the Atlantic coast (ATL1 and ATL2). Each region included different numbers of survey sites for which temporal trends were available (i.e. with sites monitored twice at least five years apart). "Communities" were defined as the species assemblages recorded at the sites in the different regions. Species similarity was estimated from the ultrametric functional tree taken from Thuiller *et al.* (2014) based on body mass, diet and feeding behaviour (see Appendix S4 for details). Each community was given the same weight.

Mathematically, this means that for all s and t , $\omega_{st} = \frac{1}{ST}$. To further facilitate the interpretation of the result of the spatio-temporal decomposition, we used a double principal component analysis (*dpcoa*, Pavoine *et al.* 2004) to visualise the differences between the sites in each region in terms of functional composition (Appendix S5 and Figure S2). A summary of the information on the four regions is available in Table 2.

Results

Spatial β -diversity

Absolute values of spatial β -diversities differed strongly between the four regions (Figure 4). We found that MED2>ATL2>MED1>ATL1 regarding spatial β -diversity. When focusing on standardised β -diversity, the ranking between regions changed: the spatial β -diversity of the region MED2 (which contained 14 sites) appeared much smaller (decreased rank) such as ATL2>MED1>MED2>ATL1. This was confirmed by the multivariate analysis, where MED2 appeared less spatially structured across the main multivariate axis compared to the other regions (Appendix S5, Figure S2). The region MED1 and the region ATL2 stood out for their high values of standardised spatial β -diversity which indicated that the time pools were more distinct in these regions than in the other two regions. This difference could be due to greater region-wide environmental heterogeneity in MED1 and ATL2 compared to MED2 and ATL1. The null model made it possible to determine that the site pools of the region MED1 were more functionally different (albeit marginally) than expected from their taxonomic composition compared to ATL2 despite having a lower standardised value of spatial β -diversity (MED1, effect size of $\beta_S = 1.22$; ATL2, effect size of $\beta_T = 0.21$; Figure 4). The multivariate analysis of MED1 (Figure S2) further suggested that sites at both dates were differentiated mainly according to the body size of their constituent species, suggesting a degree of large-scale environmental filtering acting on the birds' functional traits. On the other hand, the difference between the ATL2 site pools was not significantly different from the random expectation. This suggests that the large functional difference between site pools was due to a large number of different species (hence the high spatial β -diversity) but that between the site pools these species were not particularly distinct in terms of their functional traits.

Temporal β -diversity

Overall, the temporal change in regional diversity was more substantial in the two Mediterranean regions than in the two Atlantic regions (Figure 4). However, the use of the null model showed that the temporal β -diversity in MED1 was much higher than expected from the taxonomic change (effect size = 3.09) while in MED2, the temporal β -diversity was only marginally different from the taxonomic change (effect size = 1.48). This showed that between the two dates studied, the MED1 time pools were significantly different in terms of the functional traits of their constituent species (as suggested by the multivariate analysis, this was most likely due to the relative increase in larger-bodied species in all the sites over time, Figure S2). In contrast, the two Atlantic regions showed low temporal β -diversity, and the null model further showed that it was even lower than expected from the taxonomic change for ATL1 (ATL1, effect size of $\beta_T = -1.87$; ATL2, effect size of $\beta_T = 0.15$; Figure 4). This indicated that the sites studied in ATL1 remained remarkably constant over time, with species being substituted by other species with similar functional traits. Overall, these results are consistent with previous diachronic analyses, which demonstrated substantial changes in bird communities in inland Mediterranean areas over time due to major changes in land use (Preiss *et al.* 1997; Sirami *et al.* 2007).

Interaction term

The interaction term β_{ST} was always higher than 1 across the four regions studied. However, as the value of β_{ST} is dependent on both β_T and β_S and the study design (number of sites and number of dates), it was difficult to compare it across regions. The null model provides a way of determining whether the interaction term was higher or lower than expected from the taxonomic turnover. We found that the interaction term of β_{ST} was much higher than expected (effect size = 1.99) indicating that individual sites changed more in functional composition than expected from the temporal trend at regional level (β_T). Furthermore, the case of ATL1 is interesting because while β_S and β_T are both lower than expected, β_{ST} is marginally higher than expected (effect size = 0.26). We interpreted this as a case of a region with communities whose functional composition had changed markedly over time, but in opposite directions. This indicates potential for investigating β_{ST} as an emergent spatio-dynamic component of community changes.

Perspectives and limitations of spatio-temporal decomposition

The novel methodology presented herein has several advantages and strengths. Firstly, it allows a standardised decomposition of diversity across regions with potentially very different γ -diversities. In France, the functional and phylogenetic γ -diversities of avifauna are heterogeneous across space due to different macro-climatic influences (Devictor *et al.* 2010). Most notably, the Mediterranean Basin has high taxonomic, functional and phylogenetic γ -diversity, which contrasts with the rest of France. Using our methodology, β -diversities are found to be pairwise independent from the local γ -diversities, thus making it possible to study processes such as landscape heterogeneity or land use change across regions without interference from the biogeographical differences quantified by the γ -diversities. In contrast, there was a risk with the original *Anodiv* procedure (Rao 1986) of yielding overestimated values for β -diversities in biogeographical areas with high γ -diversities, regardless of the actual spatial or temporal change (Baselga 2010).

Secondly, our methodology accounts for differences in sampling efforts between regions. In our case study, spatial and temporal functional β -diversities were standardised using the maximum and minimum value they could possibly attain in a region (Figure 4), thus producing estimates of β -diversities that were unrelated to the number of sites or dates studied within each region (Chao *et al.* 2012). Although our method does not prevent bias if the sampling is not representative of the biodiversity in a region over space and time, the standardisation makes it possible to compensate for an unbalanced study design between regions. This solves a common problem arising from large-scale biodiversity monitoring where remote areas tend to be under-sampled (Jiguet *et al.* 2012; Ficetola *et al.* 2013).

Thirdly, our approach also makes it possible to test the space-for-time substitution often used when time-series data are not available. The drivers of diversity change such as climate (e.g. Blois *et al.* 2013) or land use (e.g. Sirami *et al.* 2007) can be studied both across space and time. Ecologists have thus traditionally used space-for-time substitution as an alternative to expensive and rare long-term studies (Pickett 1989; e.g. Chalmandrier *et al.* 2013). This substitution assumes that changes in diversity over spatial locations and changes in diversity over time are equivalent and independent under the assumption that they are driven by the

same ecological process (Fukami & Wardle 2005). However, this assumption can easily be violated by confounding processes such as dispersal (Brotons *et al.* 2005), biotic interactions (Thuiller *et al.* 2007) and delayed responses to changes in the local environment (Devictor *et al.* 2012). Our methodology provides tools which are adapted to testing the assumption on which space-for-time substitution is based: the pairwise independence of β_S and β_T allows for the direct comparison of the spatial and temporal components of changes in diversity. However, we showed that this independence property was only maintained if the sampling design is balanced (i.e. there is relatively a low amount of missing data and communities have a similar weight). We therefore recommend testing the sampling design beforehand using the simulation procedures to assess whether β_S and β_T are theoretically pairwise independent.

Fourthly, this is the first study to adapt the diversity decomposition between multiple factors originally proposed by Rao (1986) to the requirements of β -diversities computations, as recommended by Jost (2007) and Tuomisto (2010). Furthermore, we generalise this approach using Chao's index (2009) which includes species' functional and phylogenetic distances, thereby combining the advantages of both methods. Shannon entropy exponential and its generalisation are the only equivalent numbers that fully combine the properties of the additive and multiplicative α , β , γ decomposition (Jost 2007). This opens promising avenues for adapting our framework to methodologies based on the additive decomposition of the Shannon entropy (e.g. Pelissier & Coueron 2007). It is also the only equivalent number where 1) there is more or less a general consensus about the handling of unequal weighting of communities (but see Chiu *et al.* 2014) and 2) the unequal weighting still leads to β -diversities values that are pairwise independent from γ and α -diversities (Jost 2007, Tuomisto 2010).

Chao's index belongs to a large family of indices that extend the Hill numbers (1973) to include species' phylogenetic similarities (Chao *et al.* 2010) making it possible to explicitly parametrize the weight given to a rare vs. a dominant species. While our framework is transposable to these indices, some properties (pairwise independence of β -diversities from γ and α -diversities, range of β_{ST} and of nested β -diversities) need to be demonstrated, in particular in the case of missing data and unequal weighting of communities. The Chao's index studied is based on assumptions on how to take into account species abundances, i.e. the contribution of a species to the diversity value is proportional to its relative abundance (Chiu *et al.* 2014). It thus may not be suitable for achieving certain analytical aims: for instance, a conservation approach may want to consider rare and dominant species equally regardless of their relative abundance. On the other hand, a focus on ecosystem functioning may require an emphasis on dominant species as they are expected to be the main contributors to ecosystem functioning (Garnier *et al.* 2004; but see Mouillot *et al.* 2013). Furthermore, recent work has shown the value of analysing diversity patterns with multiple equivalent numbers in order to vary the weighting given to dominant as opposed to rare species, and to disentangle multiple assembly rules (Arroyo-Rodriguez *et al.* 2013; Chalmandrier *et al. in press*). We therefore argue for more statistical development to adapt spatio-temporal decomposition to other equivalent numbers, using the generalisation of Hill

numbers, and thus adding a supplementary parameter which explicitly examines the impact of species' relative abundances.

Conclusion

Recent years have seen major efforts to unify methodologies for evaluating and decomposing assemblage diversity. We have drawn on these achievements to propose a methodology that overcomes the challenges encountered when studying large-scale diversity datasets which encompass multiple orthogonal dimensions. We have shown that this approach can be used with classical animal survey data (also available for butterflies, fishes and plants) and that it provides clear results. Although more work is required to expand this method to multiple diversity indices, we believe that the properties of our methodology open up promising avenues for evaluating and testing diversity change across multiple dimensions. This will allow thorough analyses of the ever-increasing data produced by biodiversity survey programs worldwide.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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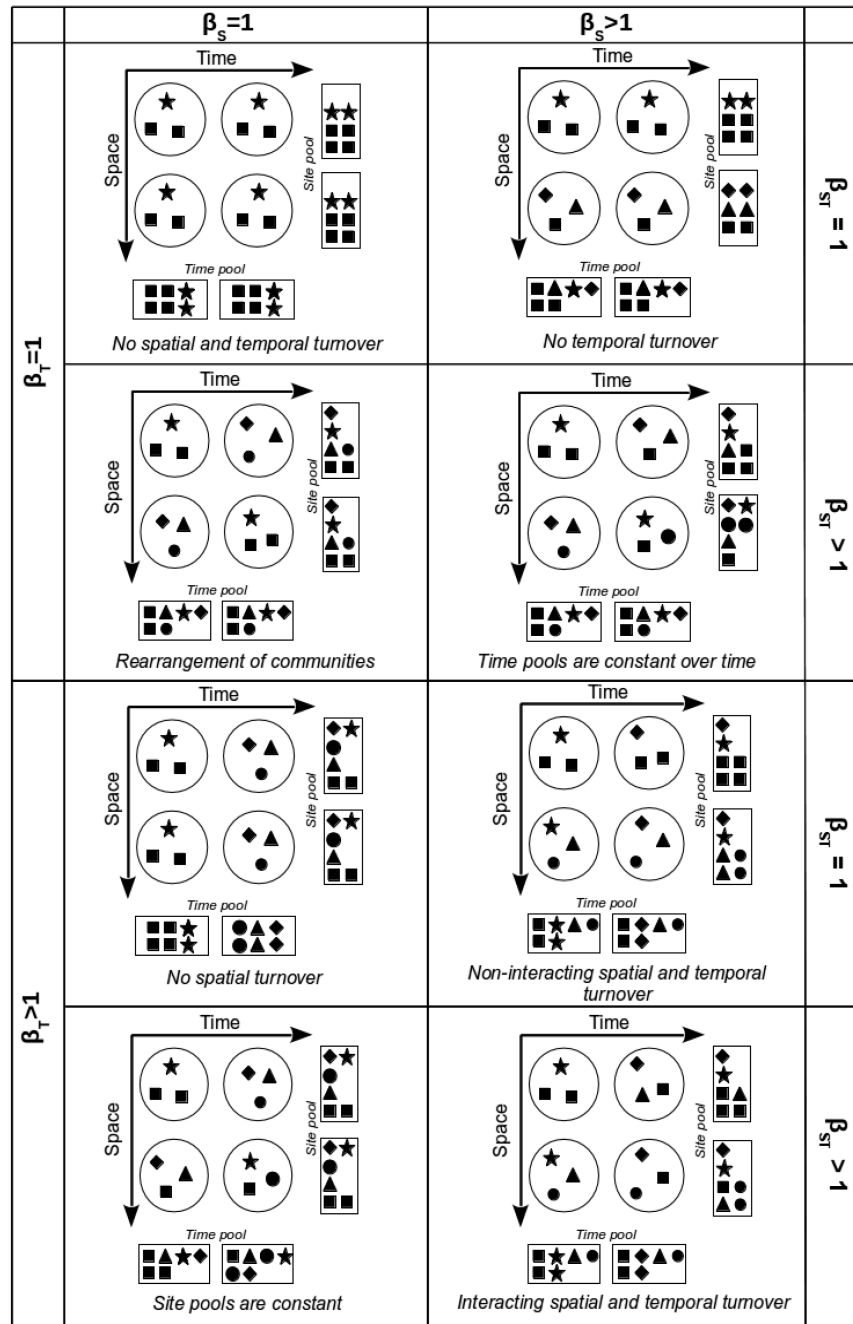


Figure 1. Graphical interpretation of the eight possible patterns of diversity change over space and/or time and their respective β_S , β_T , β_{ST} value. Each cell of the table represents one of the patterns illustrated by the composition of four communities from two sites (lines) at two dates (column), each represented by a circle. Sites and time pools (see Methods) composed from the pooled composition of communities over sites or dates, respectively, are represented by rectangles. Within communities and pools, symbols represent individuals from a species specified by the geometrical shape.

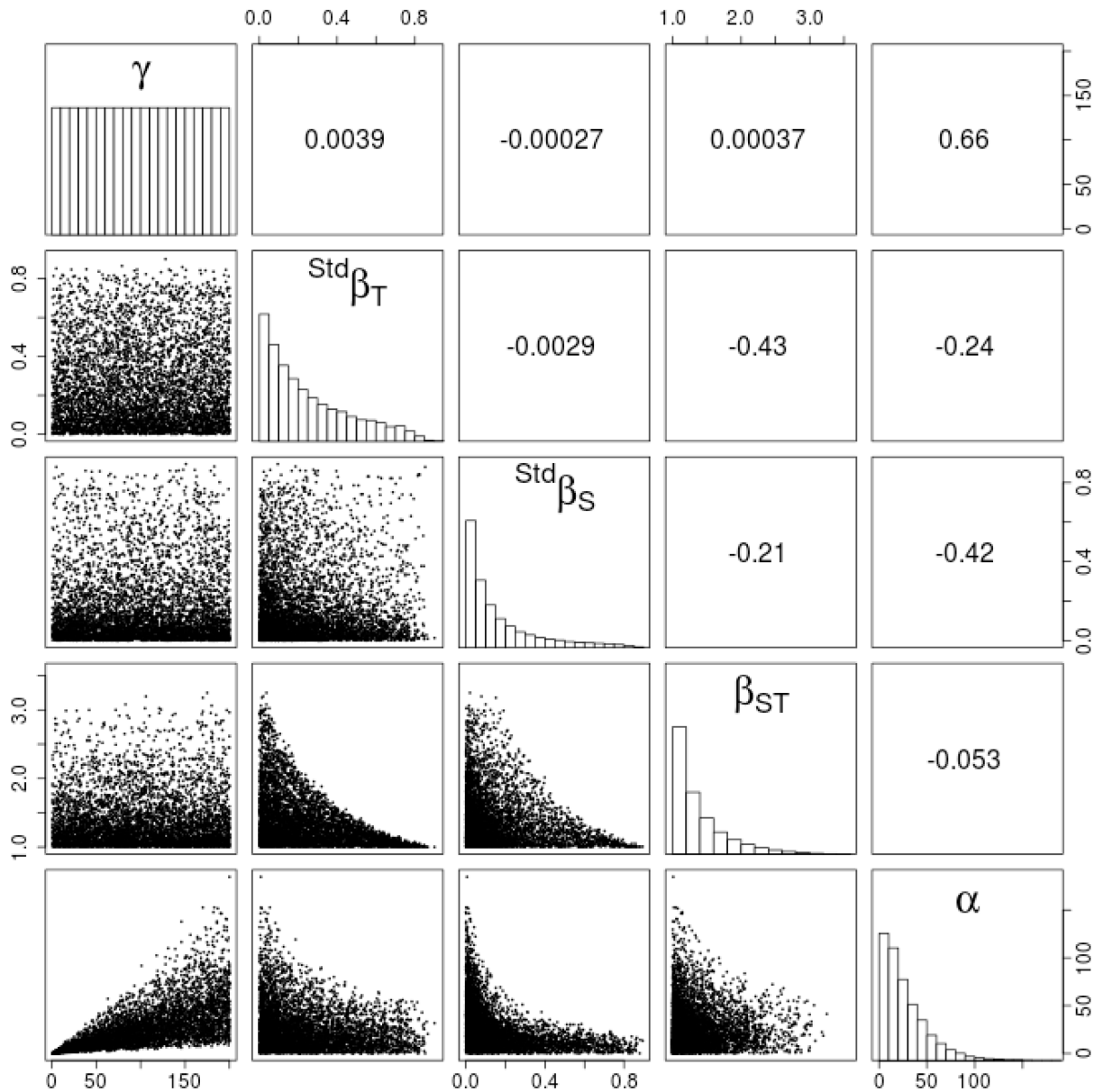


Figure 2.

Pairwise scatterplot of the value of γ , $\text{Std}\beta_T$, $\text{Std}\beta_S$, β_{ST} and α obtained from a “top-down” simulation procedure. T was equal to 4 and S to 10. The panels on the diagonal represent the distribution of each diversity estimate over the simulations. The panels from the lower triangle represent the pairwise relationship between two of diversity estimates and the panels from the upper triangle contain the Pearson correlation coefficient between two of diversity estimates.

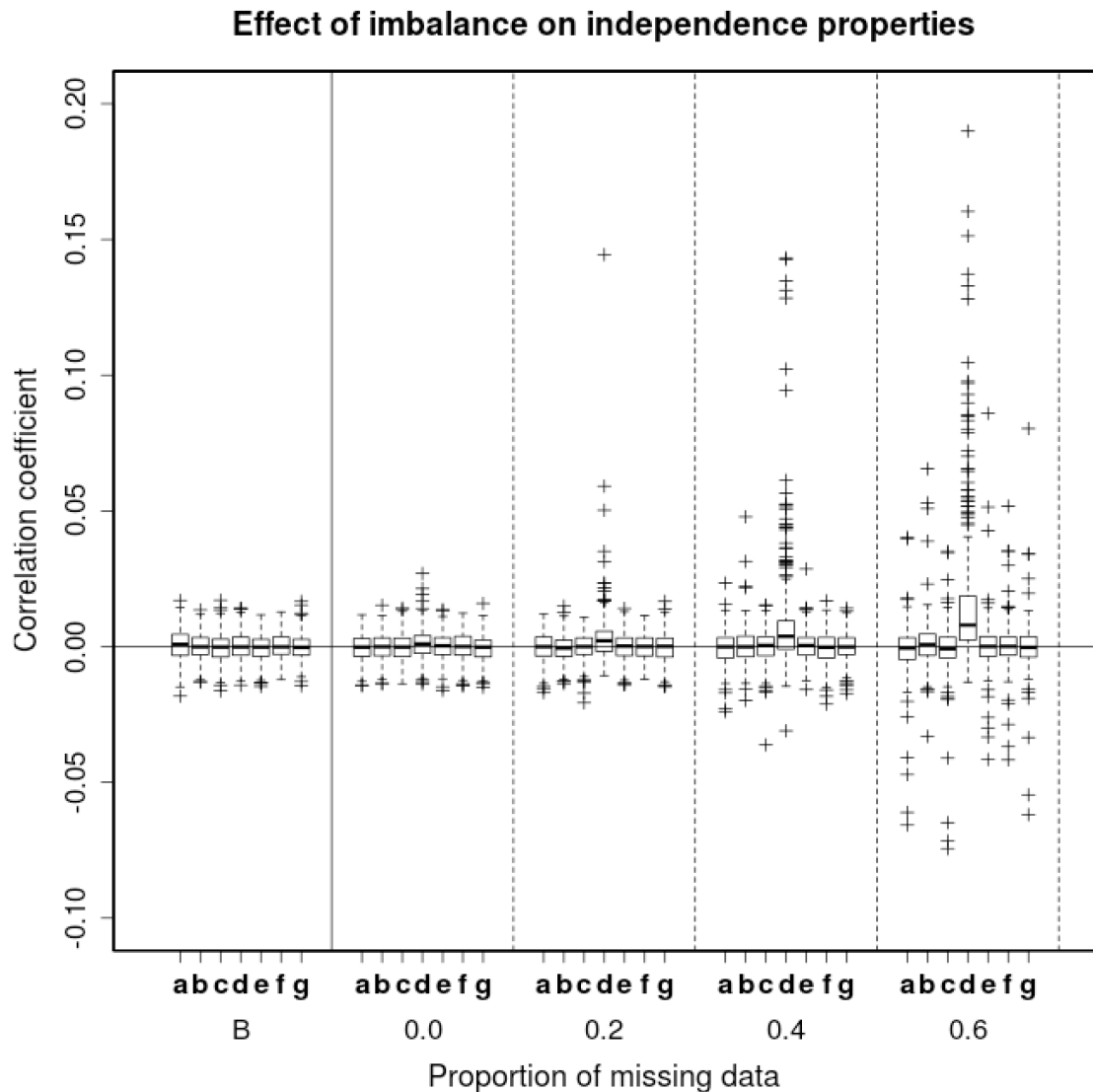


Figure 3.

Boxplots of the correlation coefficients obtained from the simulations as a function of the percentage of missing data (e.g. community weights set to 0). The boxplot on the far left (designated by “B”) illustrates the case of perfect balance (all community weights are equal). The figure displays the correlations between (a) γ and $\text{Std}\beta_T$ given by the top-down procedure, (b) γ and $\text{Std}\beta_S$ given by the top-down procedure, (c) γ and β_{ST} given by the top-down procedure, (d) $\text{Std}\beta_T$ and $\text{Std}\beta_S$ given by the top-down procedure (e) $\text{Std}\beta_T$ and α given by the bottom-up procedure, (f) $\text{Std}\beta_S$ and α given by the bottom-up procedure and (g) β_{ST} and α given by the bottom-up procedure.

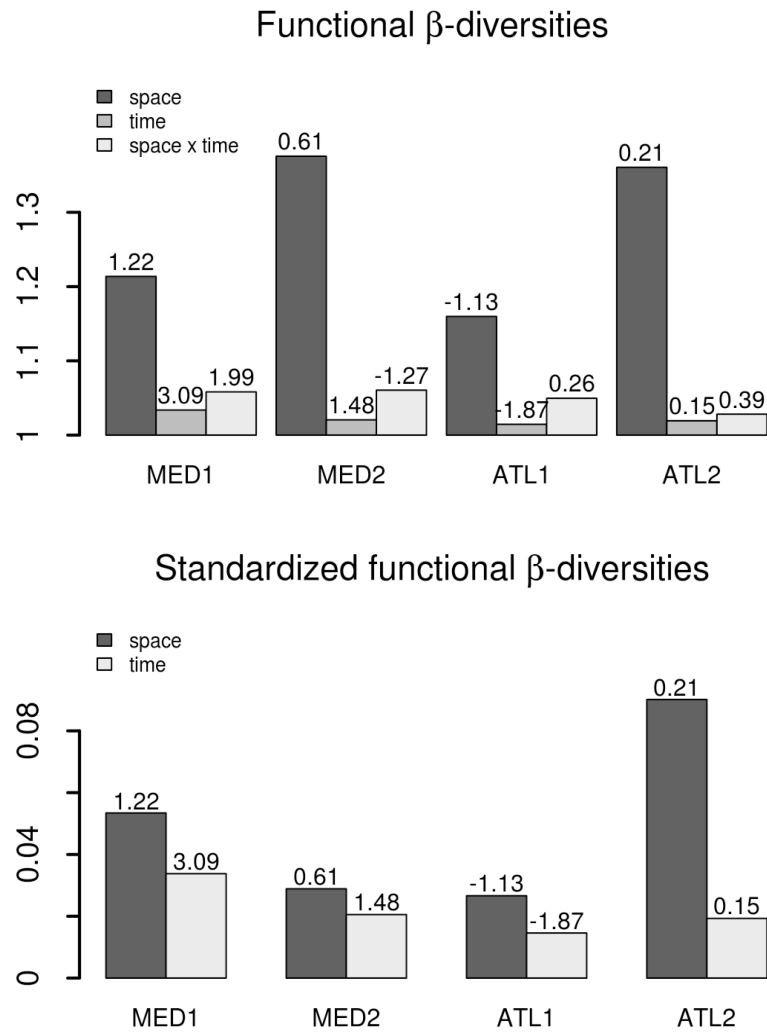


Figure 4.

Functional 1 β -diversity decomposition between spatial (dark-grey), temporal (grey) and spatial-temporal interaction (light-grey) components for each of the four regions. Each bar represents the absolute value of the β -diversity (top) or its value standardised by its minimum and maximal possible value (bottom). Numbers above each bar show the effect size against the null model. A negative value indicates a higher than expected value of β -diversity while a positive value indicates a lower than expected value of β -diversity.

Table 1

Correlation coefficients between diversity measures according to the simulation procedure for a given T and S value. The table displays the range of coefficients over the tested values of T and S ($2 \leq T \leq 10$; $2 \leq S \leq 10$). Asterisks indicate correlation coefficient intervals close to 0.

Diversity measures	Top-down approach	Bottom-up approach
γ and $\text{Std}\beta_T$	[-0.0143, 0.0117]*	[0.149, 0.598]
γ and $\text{Std}\beta_S$	[-0.0137, 0.0153]*	[0.146, 0.596]
γ and β_{ST}	[-0.0137, 0.0142]*	[-0.181, -0.0653]
γ and α	[0.485, 0.912]	[0.485, 0.915]
$\text{Std}\beta_T$ and $\text{Std}\beta_S$	[-0.0137, 0.0270]*	[-0.107, 0.193]
$\text{Std}\beta_T$ and β_{ST}	[-0.559, -0.0725]	[-0.414, -0.185]
$\text{Std}\beta_T$ and α	[-0.486, -0.111]	[-0.0162, 0.0136]*
$\text{Std}\beta_S$ and β_{ST}	[-0.560, -0.0695]	[-0.415, -0.188]
$\text{Std}\beta_S$ and α	[-0.490, -0.106]	[-0.0145, 0.0124]*
β_{ST} and α	[-0.182, 0.0206]	[-0.0150, 0.0159]*

Table 2

Characteristics of the different regions.

Region	Biogeographical zone	Number of sites	First year	Final year	Size of the species pool	Functional γ -diversity	Functional α -diversity
MED1	Mediterranean	5	2003	2008	63	8.06	6.48
MED2	Mediterranean	14	2003	2009	57	10.75	7.22
ATL1	Atlantic	7	2003	2009	43	8.32	6.73
ATL2	Atlantic	5	2003	2009	44	8.69	6.10