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► To cite this version:

Sandrine Pavoine. adiv: An r package to analyse biodiversity in ecology. *Methods in Ecology and Evolution*, In press, <10.1111/2041-210X.13430>. <hal-02915417>

HAL Id: hal-02915417

<https://hal.science/hal-02915417v1>

Submitted on 18 Aug 2020

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adiv: an R package to analyse biodiversity in ecology

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Running headline: adiv: an R package to analyse biodiversity

Article type: Applications

Abstract

1. R is an open-source programming environment for statistical computing and graphics structured by numerous contributed packages. The current packages used for biodiversity research focus on limited, particular aspects of biodiversity. Most packages focus on the number and abundance of species.

2. I present an R package named `adiv` that provides additional methods to measure and analyse biodiversity. `adiv` contains approaches to quantify species-based, trait-based (functional) and phylogenetic diversity (i) within communities (α diversity), and (ii) between communities (β diversity), and (iii) to partition it over space and time (α , β , and γ levels of diversity). Partitioning approaches allow evaluating whether the levels of α and β diversity could have been obtained by chance. Moreover, groups of biological entities (e.g., species of

the same clade or with similar biological characteristics) that drive each level of diversity (α , β , and γ) can be identified via ordination analyses.

3. Although the package focuses on interspecific diversity in its current state, the developed approaches can also be applied to analyse intraspecific diversity or, at another level, ecosystem diversity. More generally, the functions can be applied in any discipline interested in the concept of diversity, such as economics or linguistics. Indeed, all available approaches can be easily applied at other scales and to other disciplines provided that the data have the required format: a matrix of abundance or presence/absence data of some entities in some collections and information on the differences between the entities.

4. `adiv` aims to complement existing R packages in order to provide scientists with a wide variety of diversity indices, as each index reflects a very specific facet of biodiversity. `adiv` will grow in the future to integrate as many validated approaches for biodiversity analysis as possible, not yet available in R. As it includes both traditional and recent viewpoints on how biodiversity should be evaluated, `adiv` offers a promising platform where methods to analyse biodiversity can be developed and compared in terms of their statistical behaviour and biological relevance. Applications of the most relevant tools for a given study aim will eventually improve research on human-driven variations in biodiversity.

KEYWORDS: biodiversity, community ecology, conservation, diversity apportionment, diversity measurement, functional trait, phylogeny, software

1 | INTRODUCTION

The package named `adiv` (for Analysis of bioDiversity) focuses on the measurement of biological diversity (or biodiversity, the variability in life from genes to ecosystems) and on the analysis of its organization in space and/or time. I developed `adiv` in the open-source R environment for statistical computing and graphics (R Core Team, 2019). Although this environment is rich in contributed packages, most of those that focus on biodiversity, which include approximately 40 packages (among the 15300 current packages, R Core Team, 2019), actually concentrate on *species diversity* (see Table 1 for a glossary with the definitions of the expressions in italics). A few other packages (e.g., `FD` Laliberté, Legendre, & Shipley, 2014; `TPD` Carmona, 2018) focus on *functional diversity*, while others (e.g., `PhyloMeasures` Tsirogiannis & Sandel, 2017) are dedicated to *phylogenetic diversity*. More generally, some packages, e.g., `entropart` (Marcon & Herault, 2015), focus on species, phylogenetic and functional diversity and consider a limited number of diversity indices. Only a few packages focus on other aspects of biodiversity; for example, `diveRsity` (Keenan et al., 2013) evaluates genetic diversity in the context of population genetic analyses.

`adiv` enriches the total library of biodiversity packages by providing both traditional statistical approaches to diversity (e.g., Hill, 1973) and recent approaches that measure *trait-based* and *phylogenetic diversity* (e.g., Faith, 1992; Chao et al., 2010; Pavoine, Love, Bonsall, 2009; Pavoine, Baguette, Bonsall, 2010; Kondratyeva et al., 2019; Pavoine & Ricotta, 2019). In addition, all approaches can be easily applied to other aspects of diversity. Indeed, `adiv` relies on the following principle: biodiversity emerges from the differences between entities, regardless of the entities selected (e.g., species, individuals, genera or assemblages) and the criterion used to evaluate the differences between the selected entities (e.g., morphology, behaviour, evolution). The main functions of `adiv` permit the quantification of species-based,

trait-based and phylogenetic diversity within communities (α diversity) and between communities (β diversity). They complement these measurements that partition the diversity over all communities (γ diversity) with ordination methods to identify groups of biological entities (e.g., species of the same clade or with similar biological characteristics) that drive levels of diversity (Figure 1). The package is available on CRAN (<https://cran.r-project.org/web/packages/adiv/index.html>). As an R package, it is open-source to encourage transparency in science, as all codes can be freely read and checked.

2 | DATA SETS

The functions in `adiv` typically work on a matrix of species presence-absence or abundance data in *communities* and on species trait data and/or phylogenetic (or taxonomic) data (Figure 1). Data that characterize communities can also be included, such as environmental, spatial or temporal data. As trait-based and phylogenetic aspects of diversity are often compared in ecological studies, the `adiv` package implements a few functions to test if closely related species share similar traits (*phylogenetic signal*, functions `rtestdecdiv`, `K`, `Kstar` and `Kw`).

For illustrative purposes, `adiv` currently contains eight data sets. One of these data sets, named `batcomm`, is used below to illustrate some of functions of `adiv`. `batcomm` is a list of two components: `batcomm$ab` contains the abundance of 34 bat species in four habitats (rainforests, cacao plantations, old fields, and cornfields) in the Selva Lacandona of Chiapas, Mexico (data collected by Medellín, Equihua, & Amin, 2000); `batcomm$tre` contains a phylogenetic tree. The tree is ultrametric, meaning that the total branch length from any tip (species) to the root remains constant.

3 | DIVERSITY INDICES

3.1 | Species diversity

`adiv` contains two main functions for *species diversity* indices: `speciesdiv`, which includes widely used indices such as *species richness* and the Shannon (1948) index, and `divparam`, which includes indices that have a parameter to control the importance given to rare versus abundant species in diversity measurements. As an illustration, using `divparam`, I applied Hill (1973) numbers to the bat dataset. Note that all scripts used in this paper are available in the `adiv` vignette (Pavoine, 2020), named "adiv Package User Guide", that can be accessed from the R console by using the following script: `browseVignettes("adiv")`. As a traditional diversity index, the Hill index increases with species richness and evenness in species abundances. Its parameter, denoted q , increases with the importance given to abundant species compared to rare species in diversity measurement ($q=0$ means species richness, i.e., equal importance to all species). According to the Hill index, the rainforest dominates in terms of species diversity; however, variations among the diversity levels of the other three habitats indicate how the consideration of abundance data may influence our interpretation of the impact of environmental disturbance on biodiversity (Figure 2a).

With species diversity indices, species are implicitly considered interchangeable because only the number and/or abundance of species is important, not their identity. An assemblage of three bird species, say, a blackbird, sparrow and pigeon, would be considered as rich as an assemblage with three species of different groups, say, a blackbird, domestic cat, and common wall lizard. In contrast, by considering phylogenetic analysis rather than strictly presence- or abundance-based analyses, a higher value of diversity could be attributed to the second assemblage than to the first as the species in the second are more phylogenetically distinct and have more divergent biological characteristics or traits.

3.2 | From species diversity to phylogenetic diversity

In the `adiv` package, four main functions consider the phylogeny of species when measuring their diversity. Among them, `evodiv` and `evodivparam` consist of replacing species in traditional diversity indices (for `evodiv`) and traditional parametric diversity indices (for `evodivparam`) with branch units or "features" on phylogenetic trees where species are the tips (Faith, 1992; Pavoine & Ricotta, 2019). It is assumed that the number of features supported by a given branch of a phylogenetic tree is equal to the length of that branch, such that the richness of features in a community is Faith's widely used phylogenetic diversity index (Faith, 1992). The abundance of any feature on a given branch of the phylogenetic tree is measured as the summed abundance of all tips (species) descending from that branch. This approach of replacing species by features is simple and can be applied to all diversity indices developed so far. For example, phylogenetic data can be simply added to the analysis of the bat communities using the `evodivparam` function. The results, which are displayed in Figure 2b, show that when abundant species are given high weight ($q > 2$), all habitats reach similarly low levels of phylogenetic diversity, indicating that, within each habitat, abundant species tend to be closely related.

3.3 | Trait-based diversity

The indices dedicated to phylogenetic diversity can be used with trait-based data if a dendrogram is established, for example, by applying a clustering approach to a matrix of trait-based differences between species. Three other functions in `adiv` allow the measurement of diversity using direct trait-based differences or similarities between species: `QE`, `qHdiv` and `Rentropy`. `QE` implements Rao's quadratic entropy (1982), which is the average abundance-weighted trait-based difference between any two species in a community. The more different the traits of any two individuals in a community are, the higher the quadratic entropy is. `Rentropy` is equivalent to `QE` but species' relative abundances are squared-root transformed

before calculation. Both `QE` and `Rentropy` generalize well-known species diversity indices to include trait-based data: `QE` generalizes the Simpson (1949) index, which is a simple function of the Hill index if its parameter q equals 2, and `Rentropy` is a direct generalization of the Hill index when $q=0.5$. `qHdiv` allows, when required, intraspecific variation in biological trait values to be considered.

These (dis)similarity-based indices can inversely also be used to evaluate phylogenetic diversity if phylogenetic (dis)similarities are used instead of trait-based (dis)similarities. For example, with the bat dataset, I calculated cophenetic distances (sum of branch lengths along the shortest path) between species on the phylogenetic tree and used them in functions `QE` and `Rentropy` (Figure 2c). With `QE`, all habitats had similar levels of phylogenetic diversity, which is in accordance with the results obtained above with function `evodivparam` if parameter q equals 2 (Figure 2b). With `Rentropy`, the rainforest dominates in terms of phylogenetic diversity, with cacao plantations and old fields having intermediate values and cornfields having the lowest value, which is in accordance with the results of function `evodivparam` if q approaches 0.5 (Figure 2b).

4 | DISSIMILARITY INDICES

The concepts of diversity and (dis)similarity are linked: the diversity of an assemblage is null if all its components are identical. The biodiversity of a region increases with the increase in the dissimilarities between species and also between communities. Indices of dissimilarity thus complement those of diversity in `adiv`.

4.1 | From species-to-species to community-to-community dissimilarity indices

171 A few functions are dedicated to the calculation of dissimilarities or similarities between
172 species using trait, taxonomic or phylogenetic data (e.g., `CFprop`, `CFbinary`, `dsimFun`,
173 `dsimTax`, and `dsimTree`). These functions lead to particular mathematical properties for the
174 (dis)similarities between species. These properties named "positive semidefinite" for
175 similarity matrices and "Euclidean" for dissimilarity matrices are exploited, for example, in
176 the `dsimcom` function of `adiv` (see details in the `adiv` vignette named "adiv Package User
177 Guide"). `dsimcom` implements the Pavoine and Ricotta (2014) index of similarity between
178 two communities by comparing their species lists, the abundances of each species and the
179 functional or phylogenetic similarities between the species. This function is restricted to
180 matrices of similarities between species that are said positive semidefinite. Other indices of
181 the (dis)similarity between two communities can integrate any matrix of (dis)similarities
182 between species without any restrictions on their mathematical properties apart from having
183 nonnegative values and sometimes being bounded between 0 and 1. This is the case, for
184 example, for the indices available in the `dissABC` and `dissRicotta` functions of `adiv`.

185

186 **4.2 | From compositional dissimilarity to tree-based dissimilarity**

187 `adiv` contains two functions dedicated to phylogeny-based indices of the dissimilarity
188 between two communities: `evodiss` and `evodiss_family`. Although these functions are
189 dedicated to use with phylogenetic trees, they can be more generally applied to other tree-
190 shaped data, such as trait-based dendrograms. These functions use the feature perspective
191 described in section "3.2 | From species diversity to phylogenetic diversity", where a feature is
192 a branch unit on a phylogenetic tree. From this perspective, traditional dissimilarity indices
193 are not applied to species presence/absence or abundance data but to the presence/absence or
194 abundance of each feature. This perspective grants access to a family of dissimilarity indices,
195 and the `evodiss` and `evodiss_family` functions contain 30 key indices from this family,

including 6 parametric indices where the importance given to rare versus abundant features can be controlled. For example, applying function `evodiss` with the chord distance to the bat communities reveals that the two habitats with the most divergent phylogenetic compositions are the old field and cornfield habitats (phylogenetic dissimilarity=0.30), while the most similar habitats are the rainforest and cacao plantation habitats (0.12). Given the large number of species-based dissimilarity indices developed so far, more indices from this family could be easily added in the future depending on the needs identified in the ecological and conservation literature.

5 | APPORTIONMENT AND ORDINATION OF DIVERSITY

5.1 | Alpha, beta, and gamma diversity across space

When more than two communities are compared, the dissimilarity among them, named β diversity, complements the diversity within each community, named α diversity. The diversity of the whole set of communities (γ diversity) emerges from the combination of α and β diversity. `adiv` contains functions to partition species-based, trait-based or phylogenetic diversity in a nested hierarchy (with α , β , and γ levels; `abgdivparam`, `abgevodivparam`, `eqRao`, `eqRS`, `eqRSintra`, and `wapqe` functions). For example, `abgevodivparam` implements partitioning of Hill numbers. Applied to the bat dataset, this function shows that phylogenetic differences between the habitats mostly concern rare species, as phylogenetic β diversity decreases with parameter q (Figure 2d).

Some partitioning functions are associated with simple permutation tests to evaluate whether each level of diversity could have been obtained by chance. For example, the application of one of these tests (function `rtestEqRS`, permutation test) to the bat dataset shows that the differences in the phylogenetic compositions of the four habitats are not significant when species abundances are considered (statistic of the test, β diversity

standardized between 0 and 1 = $2.42 \cdot 10^{-2}$, P-value = 0.071), although the differences are significant when only presence/absence data are evaluated ($\beta = 2.37 \cdot 10^{-2}$, P-value = 0.049; nominal $\alpha = 0.050$). This result confirms that the most abundant species in each habitat tend to be phylogenetically similar, while phylogenetic differences occur for rare species.

`adiv` also implements a range of ordination analyses to visualize species and communities as points in a space that reveals which species contribute to the differences between communities according to their traits or taxonomic or phylogenetic positions. For example, the application of *phylogenetic correspondence analysis* (function `evoca`) to the bat dataset with presence/absence data (Figure 3) shows that cornfields were characterized by the absence of many species and many clades observed in other habitats and the presence of two closely related species: the long-tongued bats *Hylonycteris underwoodi* and *Lichonycteris obscura* (Figures 3a-c). However, the representation of the phylogenetic tree on the map of the phylogenetic correspondence analysis highlights that the phylogenetic differences between habitats are small, although significant (see entangled phylogenetic branches on Figure 3d).

5.2 | Temporal variations and crossed partitioning

Although they have thus far been mostly used in the context of spatial hierarchy, all partitioning and ordination approaches cited above could be explored to analyse the temporal variations in species, *taxonomic*, trait-based and phylogenetic *diversity*. Additionally, crossed double principal coordinate analysis (crossed-DPCoA, `crossdpcoa_maineffect`, `crossdpcoa_version1`, and `crossdpcoa_version2` functions) allows for the partitioning of species-based, taxonomic, trait-based or phylogenetic diversity between two crossed factors according to the methods in Pavoine et al. (2013). For example, 10 regions could be each followed for 5 years, resulting in space (regions) and time (years) being two crossed factors affecting diversity. Crossed-DPCoA allows the effects of space to be disentangled from the

effects of time with regard to variations in diversity level. `adiv` also allows studying spatial or temporal variations in trait-based diversity in a phylogenetic context thanks to the `decdiv` function. `decdiv` indeed implements the approach by Pavoine, Baguette, and Bonsall (2010) to partition the α , β and γ trait-based diversity across the nodes of a phylogenetic tree (see also `rtest.decdiv` function for associated permutation tests).

6 | CONCLUSIONS AND PERSPECTIVES

`adiv` focuses on ecological data to analyse species, trait-based and phylogenetic diversity. By extension, it can be used by any discipline interested in the general concept of diversity provided that the formats of the datasets are similar (at least presence/absence or abundance of any entity in any collection of entities and potentially information to characterize the differences and similarities between the entities). `adiv` will grow in the future as a state-of-the-art package for the measurement and statistical analysis of biodiversity. In particular, new developments may concern the following key points:

- **Connections with other packages on diversity.** I have written the `adiv` package to complement existing packages on diversity. Some functions contained in other packages (e.g., TPD, Carmona, 2018) are thus not available in `adiv`. Future developments could include the importation of functions from available packages to ease their calculation with the data format used by `adiv`.
- **Additions of new methodologies to measure diversity and partition it across spatial and temporal units.** Each current R package that tackles the concept of biodiversity contains only a few of the myriad of diversity indices developed so far in the literature. The consequence is that the indices are being used in scientific studies based on their accessibility in popular packages rather than based on their true scientific relevance and interest. Indeed, having these indices in a package renders

271 them more accessible for researchers for whom programming is a constraint and a
272 challenge. `adiv` aims to complement these packages to offer ecologists a wider variety
273 of diversity indices. In the interest of open science in biodiversity research, researchers
274 around the globe and from any discipline are invited to suggest critical methodologies
275 for analysing biodiversity that could be implemented in `adiv`.

- 276 • **Originality, uniqueness and redundancy.** `adiv` also complements current packages
277 by offering ways to evaluate how trait and phylogenetic information impacts
278 evaluations of biodiversity. In particular, `adiv` contains functions (`uniqueness` and
279 `treeUniqueness`) to quantify how redundant or unique a community is compared to a
280 scenario where all species would be maximally dissimilar (e.g., having the most
281 distinct values possible for biological traits). It also contains functions (e.g.,
282 `distinctDis`, `distinctTree`, `distinctTopo` and `distinctUltra`) to identify
283 species that are original in a community because they have unique states of biological
284 traits or no close relatives in the phylogeny. The presence of original species increases
285 the diversity of the community. Further versions of `adiv` will include more originality
286 indices, especially those that account for species abundances and species extinction
287 risks (see Kondratyeva, Grandcolas & Pavoine, 2019 and references therein).

288 Having all these methodologies in the same package will ease the diffusion of statistical
289 methods among all researchers and data analysts in environmental organizations interested in
290 the analysis of biodiversity. It will also facilitate comparison among methods in terms of their
291 statistical behaviour and biological relevance. All these developments in `adiv` will contribute,
292 over the years, to open science and advances in (bio)diversity research.

294 ACKNOWLEDGEMENTS

The author thanks Stéphane Dray for his help in transferring certain functions from the now deprecated class "phylog" of ade4 to the class "phylo" developed in the ape package and used in the adephylo package. She also thanks Giovanni Bacaro for co-writing the dissRicotta and rare_Rao functions and allowing their inclusion in adiv. The help files of the corresponding functions mention their contributions.

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DATA ACCESSIBILITY STATEMENT

All data used in this paper are available online in package adiv: <https://cran.r-project.org/web/packages/adiv/index.html>.

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 365

Concept	Definitions used in this paper
Community	Set of species observed at a given time in a given place.
Functional diversity	Trait-based diversity applied to functional traits (see the definition of trait-based diversity below). A functional trait is a trait that influences the way species (or organisms) respond to environmental conditions or the way they contribute to ecosystem properties.
Phylogenetic diversity	Diversity in the positions of species (or of organisms, for abundance-weighted diversity) on a phylogenetic tree. A community with many closely related species may have less phylogenetic diversity than a community with few distantly related species.
Phylogenetic correspondence analysis	Extension, proposed by Pavoine (2016), of the well-known ordination approach named correspondence analysis to include phylogenetic data.
Phylogenetic signal	Positive correlation between the differences in species trait values and the distances between species on a phylogenetic tree.
Species diversity	Number and abundance of species. Indices of species diversity increase with the number of species in a community and with the evenness in species abundances.
Species evenness	Evenness in species abundances.
Species richness	Number of species.
Taxonomic diversity	Diversity in the taxonomic relationships between species. For example, a community with many species of the same genus

	may have less taxonomic diversity than a community with few species that belong to different orders.
Trait-based diversity	Diversity in trait values. A community with many organisms that share similar trait values may have lower trait-based diversity than a community with few organisms characterized by distinct trait values.

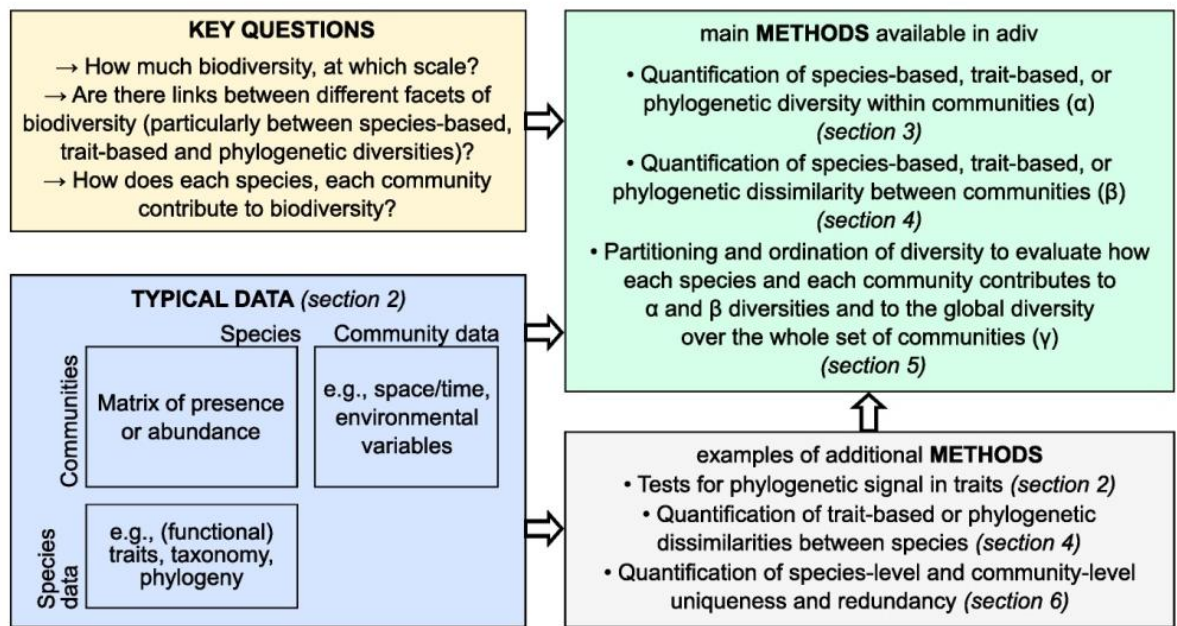


FIGURE 1 Schematic organization of *adiv*.

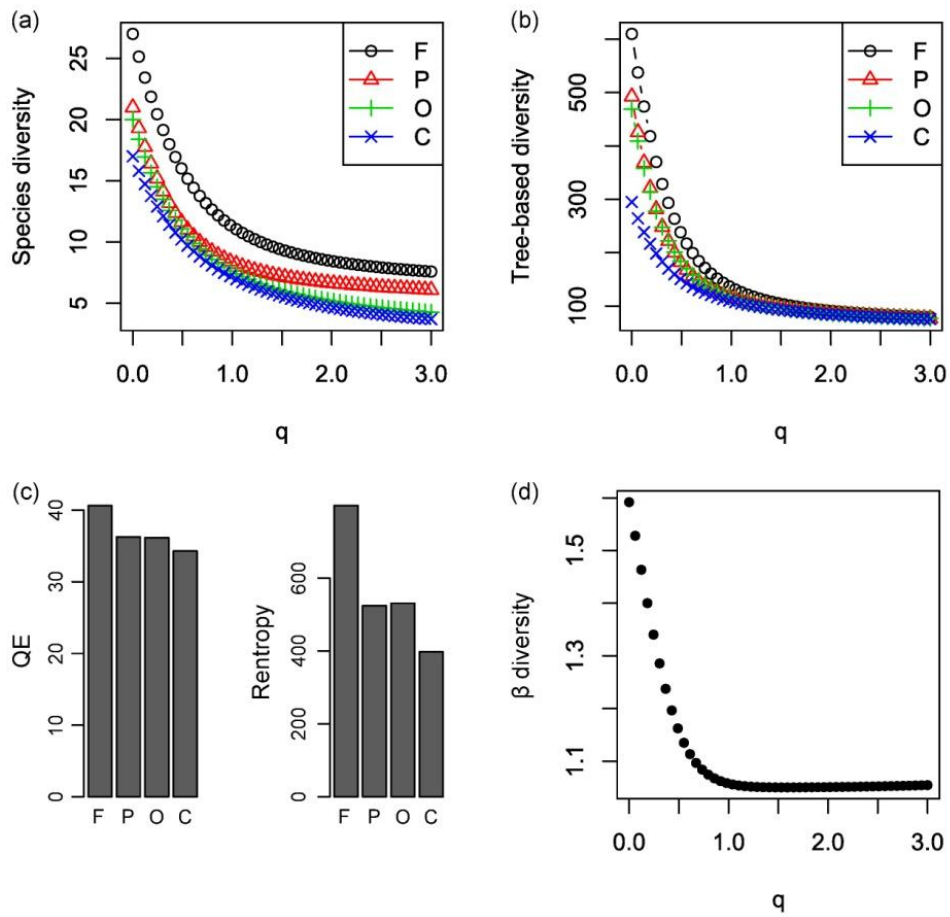


FIGURE 2 Bat species diversity (a), phylogenetic diversity (b-c) in four habitats (F=rainforests; P=cacao plantations; O=old fields; C=cornfields), and phylogenetic β diversity between the habitats (d). In panels (a), (b), and (d), the Hill index is given as a function of its parameter q . The higher q is, the less importance is given to rare species (in a) or features (in b and d) in the evaluation of diversity.

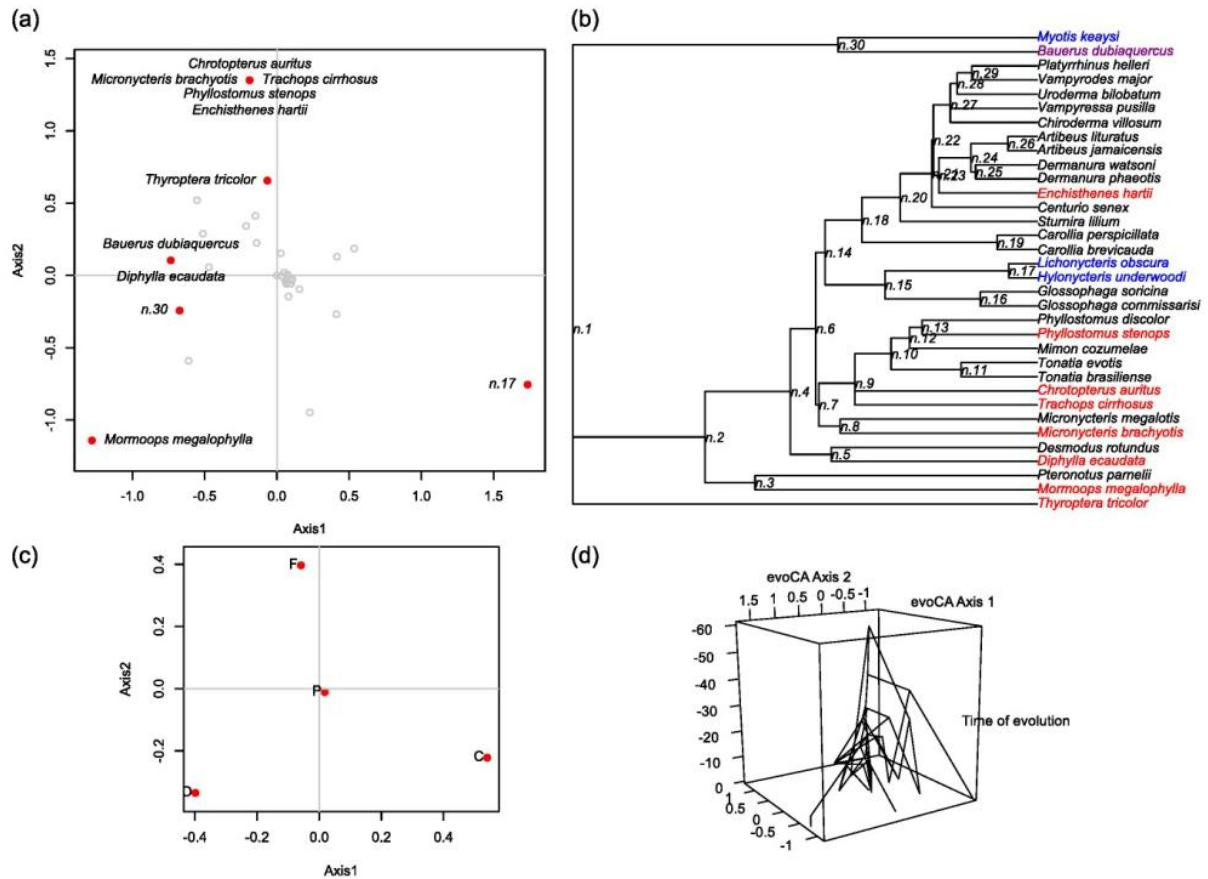


FIGURE 3 Analysis of the bat phylogenetic composition of four habitats (F=rainforests; P=cacao plantations; O=old fields; C=cornfields). (a, b, and c) Phylogenetic tree and factorial maps obtained with phylogenetic correspondence analysis (evoCA; the first axis represents 42% of the phylogenetic dissimilarities among habitats, and the second represents 37%). (a) Coordinates for the nodes of the phylogenetic tree; the positions of the "top-contributing" nodes/species (explaining more than 5% of the variance on one of the axes) are highlighted in red and labelled. (b) Phylogenetic tree (in red, top-contributing species; in blue, species descending from the top-contributing nodes; in violet, the top-contributing species that descend from a top-contributing node). (c) Coordinates for the habitats on evoCA axes. (d) 3D map of the phylogenetic tree on evoCA axes (in *adiv*, the plot is interactive).