BIODIVERSITY
BUILDING
BLOCKS FOR
POLICY

M22 Design of the phylogenetic indicators

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Summary

Short (maximum 1 page) executive summary of the milestone.

List of abbreviations

EU	European Union
IPBES	The Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services
OTL	Open Tree of Life
PD	Phylogenetic Diversity
WDPA	World Database on Protected Areas

1. Introduction

Phylogenetic diversity (PD) is a measure of biodiversity which takes evolution into account. This measure includes how evolutionary related or distinct species are and might be a good *indicator* for community functional diversity (1). It is calculated as the sum of the lengths of the phylogenetic tree branches representing the minimum tree-spanning path among a group of species (2). PD has many possible applications; it can be used as a guide for conservation purposes, as is the case for the EDGE of Existence Programme, or as a general measure for biodiversity in which we should not aim to conserve specific features, but rather to maximise a variety of features (3). The latter could be particularly useful in light of the changing environmental conditions, as we can only guess which features will be important in the future. Several studies have shown/suggested that high PD is associated with greater ecosystem stability:

- Species assemblages with high native phylogenetic overdispersion are less receptive to exotic species than the phylogenetically clustered assemblages in Himalaya (4)
- Long-term biodiversity–ecosystem function experiment at Cedar Creek, Minnesota, USA for grassland ecosystems: Effect of PD on productivity increased through time and was associated with greater ecosystem stability (5)
- Lab-experiment with 12 protist species: PD stabilises community biomass and promotes community temporal stability by reducing the strength of competition (6)

Many measures of biodiversity exist and they all have their value depending on what you want to calculate or investigate. The most intuitive one is probably **species richness**, which is defined as the number of species within a given region (7). It is easy to understand and to measure and can often be used as a surrogate for other measures that are harder to quantify (8). Based on the scale of the region, species richness is divided into three categories. Alpha diversity measures the species richness in an area smaller than the entire distribution of the species. Beta diversity looks at the change of species richness across regions. Gamma diversity is defined as the species richness in an entire region (7). Species richness, however, does not take each individual species' identity into account. It considers all species as equally valuable (3), which is more nuanced in reality. It is also more sensitive to taxonomic inflation associated with sampling effort (9).

Ecosystem functioning is probably determined by more than just the number of species, and this is where **functional trait diversity** comes in. Functional traits relate to how species acquire, share and conserve resources (10). *Violle et al.* (2007) define functional traits as "morpho-physio-phenological traits which impact fitness indirectly via their effects on growth, reproduction and survival, the three components of individual performance" (11). They can thus support both contributions to ecosystem properties and services, and tolerance to environmental stressors and disturbances (12). The lack of functional trait data for many organisms is a major limitation, whereas PD is much more feasible to calculate. As they have similar abilities to predict biodiversity effects, PD can be a valuable proxy for FD (13). Although there is increasing evidence that ecologically relevant traits show as much phylogenetic conservatism as reproductive and other taxonomic relevant traits(14–16), at least in some cases there seems to be a lack of correlation between FD & PD in a community of a given species richness (13). Due to convergent evolution it is quite possible to have a large PD and a small FD. Likewise, diversification between closely related species might mean a small PD and a large FD.

Several studies of *Cadotte et al.* have shown that PD can predict community productivity better than other measures of diversity, such as species richness or functional group diversity (1,17). Other studies even suggest that PD would promote ecosystem stability, most likely through reduced competition or increased facilitative interactions for communities with distantly related species (5,6). Based on this, it is suggested to maximise evolutionary diversity if the goal is to maximise community functionality in habitat restoration (1). On the other hand, a re-analysis of 16 PD experiments conducted in grassland ecosystems has questioned these findings. By using an updated phylogeny, they found that species richness was a superior predictor of community productivity and stability compared to PD. Although they found a significant relationship between PD and community productivity, it was not sufficiently related to ecosystem stability and was therefore concluded to be an inferior predictor compared to species richness (18).

Whether species richness, functional trait diversity, or phylogenetic diversity is the most useful measure of biodiversity, is a question of great concern to the scientific community, for which no consensus has been found yet and therefore there is a need to provide workflows that can calculate these metrics rapidly so that their behaviour can be studied under different situations and scales.

Attempts to reduce biodiversity loss are not helped by the existence of numerous measures for biodiversity, combined with a lack of consensus about which one to monitor. The Essential Biodiversity Variables (EBV) framework tries to tackle this by defining a minimum set of essential measurements to capture the major dimensions of biodiversity change (19). The difficulty of having 6 EBV classes with 21 EBV names and respective metrics is that in a real ecosystem, there will always be incomplete. According to *Lean and Maclaurin* (2016), a more general measure for biodiversity is needed for large-scale environmental decision making. They suggest conserving a maximal variety of features instead of conserving particular features. Since it is difficult to measure features directly, they suggest using PD as a general measure, as it reflects the evolutionary processes that cause functional & morphological divergence within lineages (3).

Within the maze of biodiversity measures, a multitude of PD metrics adds on to even more complexity. Luckily, *Tucker et al.* (2017) provide some clear guidelines on making informed decisions about the use of PD metrics. They collected 70 existing PD metrics and divided them into three dimensions: richness (how much?), divergence (how different?), regularity* (how regular?), which can be further subdivided according to the level of comparison (alfa or beta diversity) (20). Faith's PD index, for example, is one of the most widely used metrics of phylogenetic diversity and is defined as the sum of the length of phylogenetic tree branches representing the minimum tree-spanning path among a group of species. According to the mentioned guidelines, this metric would be categorised in the richness dimension and can be used when you want to calculate what the total evolutionary history is within (or between) assemblages.

2. Role of phylogenetic diversity in ecological processes

Community assembly

Community assembly is a very complex process for which three traditional theories exist (16). The niche theory emphasises the importance of performance-related traits and says that niche-related processes such as environmental filtering and competition determine community assembly (16,21). The theory of neutral processes, on the other hand, states that species differences and species-environment interactions are irrelevant for community assembly because species are ecologically equivalent; therefore, community assembly is a random process (16,22). A third theory brings in an evolutionary perspective by stating that community assembly is mostly determined by historical events such as speciation, adaptation, extinction, dispersal, and disturbances (16,23).

Cavender-Bares et al. (2009) present an overview of studies which revealed many different processes causing non-random phylogenetic community structure, questioning the theory of neutral processes. One of them is the study of *Maherali & Klironomos* who use an ecologically realistic model of a mycorrhizal plant community to show that species richness is highest in assembled communities that are phylogenetically overdispersed (24). Other studies consistent with the niche complementarity concept are the one of *Gerhold et al.* in which the results indicate that evolutionary history predicts the size of the regional species pool, with a larger PD leading to a larger regional species pool (25); or the one of *Chaves et al* showing a causal relationship between PD & community assembly in which there was a higher resistance of phylogenetic diverse assemblages to drought (26).

Whether PD is a driver or consequence of community assembly, is still unclear. The assessment also largely depends on the choice of the null model and taxonomic, geographic, and ecological scales (27). Nevertheless, phylogenetic information can only enrich ecological studies and allows us to consider phenomena occurring over broader temporal and spatial scales (16,28).

Nature’s contributions to people

Nature’s contributions to people (NCP) are defined by the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) as “all the contributions, both positive and negative, of living nature to the quality of life for people”. PD is recognised by IPBES as an indicator of “maintenance of options”, one of the 18 categories of NCP.
Anthropogenic drivers have widespread effects on ecosystems and their services. Traditionally, changes in NCP are predicted based on species richness, but this can only account for a part of the explanation (29). Cardinale *et al.* review two decades of research on the influence of biodiversity loss on ecosystem functions & services and state there is sufficient evidence that ecological consequences of biodiversity loss can be predicted from evolutionary history (30).

Also *Srivastava et al*. argue that community structure influences NCP through functional traits, niches, and species interactions, for which phylogeny could be a common denominator (29). The exact mechanisms of how PD is involved in NCP are only starting to be understood on an individual level, and a lot of work still needs to be done on the community level. To create a better understanding of these mechanisms, PD should be manipulated independently of species richness, something that has only been researched by *Maherali & Klironomos* so far.

To test the vulnerability of a system, *Díaz et al*. suggest correlating Specific Effect Functions, Specific Response Functions, and phylogenies. They define a Specific Effect Function (SEF) as “a species’ per unit capacity to influence an ecosystem property or service”; and a Specific Response Function (SRF) as “the ability of a species to maintain/enhance its quantity in response to specified change in abiotic or biotic environment or to invade this environment afresh”. Ecosystem functioning & services are mostly dependent on SEFs, but the correlation of SEFs, SRFs, and phylogenies could show the potential of ecosystems to deliver function under different environmental changes (12).

The utility of phylogenies in NCP depends on the strength of the phylogenetic signal of the functional traits that are relevant for the ecosystem functioning. Therefore, in case of a strong phylogenetic signal, phylogenies can be of added value to deepen the understanding of functional diversity, as PD data are more readily available (29).

Invasive species

Invasive species are among the most impactful drivers of biodiversity change (31). Several studies have been trying to find the correlation between species richness of a community and its susceptibility to invasion, leading to opposite conclusions (32,33). It has been suggested that evolutionary differences should be taken into account, but also in these kinds of studies, conflicting evidence has been found for increased susceptibility to invasion by exotic species that are more related (34) or less related (35) to native species or for communities that are phylogenetically clustered (36,37) or phylogenetically dispersed (38). *Villalobos et al.* propose to use their phylogenetic field concept, defined as the phylogenetic structure of species co-occurrence within a focal species' geographical range (39). Instead of focussing solely on site-based analyses, this approach takes into account the phylogenetic structure of the recipient assemblage (representing the site invasibility) combined with the phylogenetic relatedness between an exotic species and the recipient (representing the alien species invasiveness). *Kusumoto et al.* found mainly the following two scenarios to be true for the flora in Japan: phylogenetically clustered environments were mainly invaded by exotics from the same major clades as the native species, with environmental filtering playing a predominant role (pre-adaptation hypothesis); while phylogenetically overdispersed environments were mainly invaded by phylogenetically distinct exotics, showing a predominant role for biotic filtering (naturalisation hypothesis). They concluded that Darwin’s conflicting preadaptation and naturalisation hypotheses both apply, depending on the context (40). Naturally, there are other factors that play a role in the invasion process that are not necessarily reflected in a phylogeny, such as random dispersal, and human-mediated introduction or disturbances, but phylogenies could nonetheless be of added value to anticipate the invasibility of a recipient assemblage for individual exotic species (40).

3. Practical use of phylogenetic diversity

Slowly but surely, phylogenetic indicators are being incorporated into policy. First, some IPBES assessments have used a PD indicator as the percentage of a taxonomic group's PD that is represented by threatened species, and is recognised by IPBES as an indicator for maintenance of options. Second, the expected loss of PD is an indicator recognised by the Global Biodiversity Framework and represents the amount of evolutionary history expected to be lost in a given amount of time based on the current extinction risks faced by the set of species. Third, EDGE provides a priority list of species that are evolutionarily distinct and globally endangered. Finally, a PD Task Force exists within the framework of the IUCN, who provide leadership, guidance and expertise on the inclusion of PD in conservation strategies for practitioners, decision-makers, and the public.

These three indicators most currently used in policy, are all species-based rather than area-based. A metric that gives information about how well PD of a certain higher taxonomic group is currently safeguarded by protected areas and a spatial visualisation which can be used to identify potential directions for future expansion of protected areas is thus of particular interest. Therefore, we will design a workflow (see diagram) to calculate and visualize the overlap between protected areas and high phylogenetically diverse area. The input for the workflow will be a generated data cube of occurrences of a selected higher taxon, as well as a phylogenetic tree. We will test cubes of different resolutions in order to determine which one is appropriate, on a national level, with Belgium and South-Africa as test cases. Subsequently, the `Biodiverse` software will calculate the PD metric for each grid cell. This PD variable will be reclassified as low or high PD (see below). This output will be spatially depicted and overlayed with a layer of protected areas from the World Database on Protected Areas. The proportion of high PD areas encompassed by protected areas can then be calculated. Although we will attempt to produce an application that can visualise the evolution of this metric through time, the quality of historical data will be most likely too low to produce a reliable and usable result. An area is considered to be of high PD if it is higher than the 'expected PD'. One possible way to determine this is by using the Net Relatedness Index (NRI) and Nearest Taxon Index (NTI). For the calculation of NRI and NTI, the null model "pool.taxa.labels" (phylogeny pool) in the R library Picante could be used (41). This corresponds to a shuffle of phylogeny tip labels (across all taxa included in the phylogenetic tree). A significantly positive NRI or NTI indicates an underdispersed or clustered community that contains more phylogenetically closely related species than expected by chance. A significantly negative NRI or NTI means that the community is overdispersed; that is, it contains more distantly related species than expected by chance (36). Although this seems like a valid option, further analysis is needed to determine which method will be implemented.

It could also be useful to calculate complementarity scores to identify areas for which there are few substitute areas. PD complementarity is the sum of the additional branch length gained if an area is added to a set of areas (42).

In order to identify areas that could be protected to maximise the overall PD, we will also calculate the expected gain of PD if we protect an additional area. Likewise, we can calculate the expected loss of PD for grid cells within protected areas, to identify those areas of particular significance. Avoiding damage to these areas would minimise PD losses for little cost (43).

4. Workflow Requirements

Functional Requirements

Data Input and Validation

Phase 1:

- Ability to import GBIF occurrence data cubes. The minimum requirement is support for CSV and NetCDF format cubes. The aim is to ensure all cube formats produced by B3 are supported. (Additional potential format list: Apache Parquet, Apache Avro, GeoJSON, GeoParquet, GeoTIFF, HDF5, JSON, PMTiles, ZARR)
- Retrieval of published phylogenetic trees with branch lengths from Open Tree of Life (OTL)

Phase 2:

- When the minimum viable product has been produced, remaining time and resources will be evaluated. When possible, the product will be further developed to support importing of any occurrence data cube and any phylogenetic tree (Newick format).
- Validation of data input by the user for format, completeness, and consistency:
    - imported data cubes must have one of the supported file formats (see above)
    - data cubes must contain the following column headers: year, CellCode, speciesKey, n, minCoordinateUncertaintyInMeters
    - cellcodes must correspond to one of the supported grid systems
    - imported phylogenetic trees must be in the Newick format
    - phylogenetic trees must contain branch lengths
    - all taxonID’s in the data cube must be represented in the phylogenetic tree

Diversity Calculation

- Calculation of phylogenetic diversity metrics (e.g., Evolutionary Distinctiveness (ED), Phylogenetic Abundance (PA), Phylogenetic Diversity (PD), Relative Phylogenetic Diversity)
- Options to select the specific taxa or groups in diversity calculations
- Ability to handle large datasets and complex calculations efficiently

- Allow for the calculation of expected PD loss per species included in the dataset. Options will be made available to perform this on all species or a pre-defined subset of species.

Customization and Filtering

- Customizable parameters for phylogenetic analysis. The minimum set of adjustable parameters are:
  - selection of corresponding grid used for data cube generation
  - selection of a phylogenetic diversity metric
  - the threshold for reclassifying the diversity metrics into ‘high’ and ‘low’ classes
  - the GIS polygon layer for which the indicator is calculated (World Database on Protected Areas (WDPA) polygon layer and potentially additional layers provided, possibility to upload own polygon-layer)
- Filters for selecting subsets of data based on various criteria. The minimum set of filters that is aimed for is:
  - taxon
  - type of observation (eg. human observation or preserved specimen, i.e. dwc:basisOfRecord)

Data Export and Visualization

- Export of indicator results in CSV format
- Export of data cube with appended phylogenetic diversity metrics
- Export of diversity metrics per grid cell as a raster file, suitable for integration with GIS software
- Generation of run reports including methodology, parameters used, and interpretation of results

User Interface

- Near real-time feedback and visualisation during the analysis process
- Minimum viable product is a workflow written in R contained in a Jupyter / Rmarkdown / Databricks notebook

Error Handling and Notifications

- Robust error detection and handling for all stages of the workflow
- Notifications and alerts for process completion, errors, or required user input
- Logging of user actions and system events for troubleshooting

Scalability and Performance

- Optimised for high-performance computing environments
- Scalable to accommodate large datasets and complex phylogenies

- Efficient use of computational resources for large-scale analyses

Non-Functional Requirements

Performance

- Upon delivery of the product, hardware specifications will be provided to ensure optimal performance
- Product will be tested and estimates of expected response times will be provided to the user
- Efficient handling of large datasets without significant performance degradation

Scalability

- Ability to handle increasing data volumes or user numbers without loss of performance
- Scalable architecture to accommodate future expansion in terms of data or functionality
- Efficient resource utilisation that scales with system demand

Maintainability and Support

- Scripts and code developed for this indicator will be stored on the B-Cubed GitHub repository. Citable releases will be pushed to Zenodo
- Modular design for easy maintenance and updates
- Clear documentation for system maintenance and troubleshooting. Documentation will be stored on the B-cubed GitHub documentation website. This will include runnable code snippets..
- Folder with test datasets and repeatable test scripts on GitHub to ensure viability of software updates

Compliance and Standards

- Compliance with TDWG, data cube, and phylogenetic standards
- Adherence to best practices in phylogenetic analysis and data handling
- The ability to update if there is a need to comply with evolving standards and regulations

Portability

- Ease of system migration to different environments that support R code (e.g. Microsoft Planetary computer)
- Minimal dependency on specific hardware or software configurations

System Architecture

Description of workflow

The final product will be presented as a Jupyter, Rmarkdown or Databricks notebook which integrates the components of the workflow as runnable R scripts and documents the step-by-step process.

The workflow's architecture is presented in Figure 1.

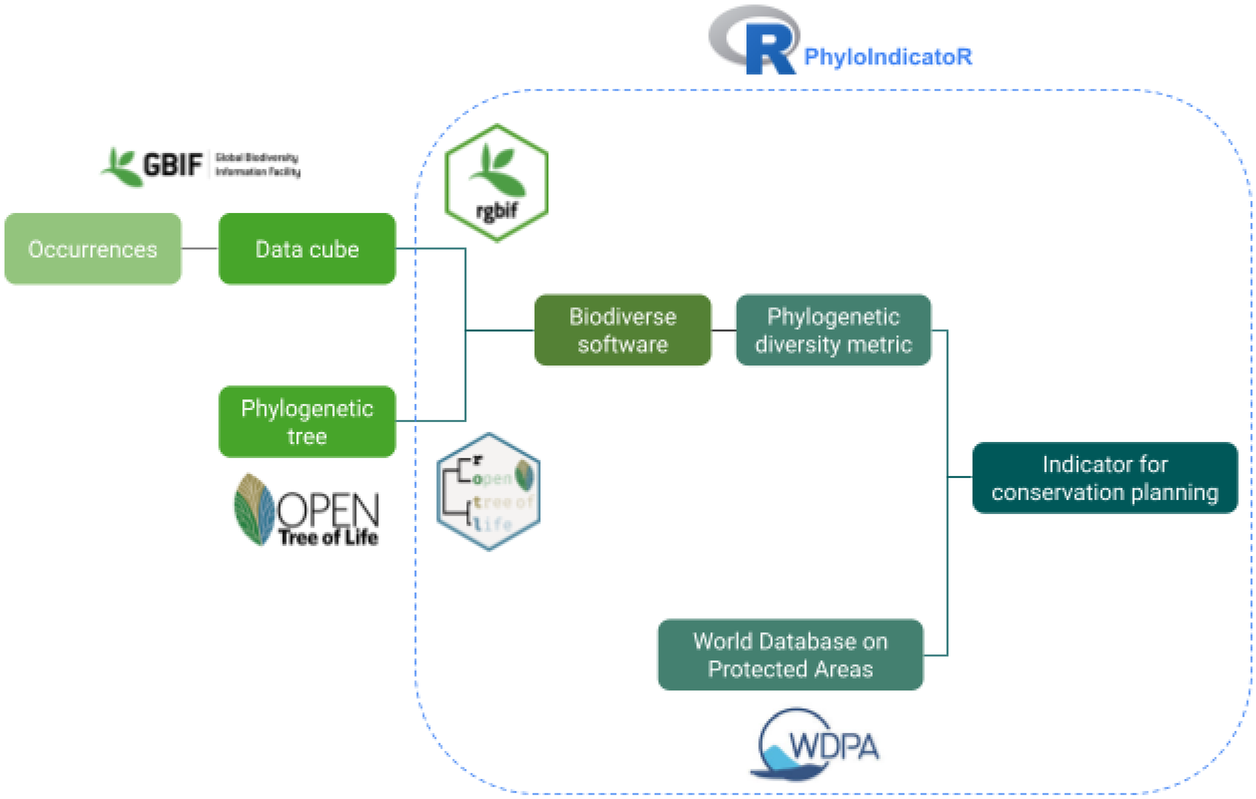

Figure 1: The components of PhyloIndicatoR, an R notebook to produce a phylogenetic indicator for conservation planning using species occurrence data cubes and a published phylogenetic tree as input.

The workflow requires an occurrence cube as input, which the user will be able to generate through the GBIF download functionality when WP2 of the B3 project is implemented. Users will be able to fully customise this cube in terms of applying data filters and adding additional dimensions. We refer to Deliverable 2.1 'Specification for species occurrence cubes and their production' (44) for more details on the options for customization that will be implemented. In addition, the user will be able to select a published phylogenetic tree with branch lengths to be imported from OTL. This will be implemented by using `rotl`, an R package to interact with the Open Tree of Life data. Alternatively, auto-retrieval of the relevant phylogenetic tree from OTL based on the taxonID's in the data cube can be implemented. Input data will then be validated for format, completeness, and consistency. The user will be offered the option to filter out certain taxa to create a subset of the data cube. Subsequently, `Biodiverse` software will be called through the `BiodiverseR` (45) package to take the data cube and phylogenetic tree as input. Users will be able to specify which phylogenetic biodiversity metric(s) will be calculated. In case PD loss (the amount of phylogenetic diversity lost when a certain taxon would disappear) is selected, the user will be able to select for which taxa this metric is calculated. `Biodiverse` will use the supplied data cube and phylogenetic tree to calculate the selected metrics for each grid cell, and the results will be written to a .csv file. The user will be prompted to select a method for determining a threshold value for the PD metric, in order to differentiate between low and high PD grid cells. The calculated values of the metrics and the boolean for low or high PD grid cell will be appended as attributes to a shapefile layer of the reference grid used in creation of the cube and overlaid with a WDPA polygon layer of protected areas. The user will also be able to upload a different polygon layer with protected areas of interest to them. The percentage of high PD area encompassed by protected areas will be calculated by performing a spatial join between the grid layer and polygon layer of protected areas. The results will be visualised as maps for each selected metric with scores per grid cell and the protected area polygons. The results with the metric scores per grid cell will also be appended to the original data cube and available for download in the supported data cube formats. The calculated values of the indicators (proportion of high PD area encompassed by protected areas and PD loss) will be exported as a .csv file.

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