mangal – making ecological network analysis simpler

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The study of ecological networks is severely limited by (i) the difficulty to access data, (ii) the lack of a standardized way to link meta-data with interactions, and (iii) the disparity of formats in which ecological networks themselves are represented. To overcome these limitations, we conceived a data specification for ecological networks. We implemented a database respecting this standard, and released a R package (rmangal) allowing users to programmatically access, curate, and deposit data on ecological interactions. In this article, we show how these tools, in conjunctions with other frameworks for the programmatic manipulation of open ecological data, streamlines the analysis process, and improves replicability and reproducibility of ecological networks studies.
Introduction

Ecological networks are efficient representations of the complexity of natural communities, and help discovering mechanisms contributing to their persistence, stability, resilience, and functioning. Most of the “early” studies of ecological networks were focused on understanding how the structure of interactions within one location affected the ecological properties of this local community. They revealed the contribution of ‘average’ network properties, such as the buffering impact of modularity on species loss (Pimm et al. 1991, Yodzis 1981), the increase in robustness to extinctions along with increases in connectance (Dunne et al. 2002), and the fact that organization of interactions maximizes biodiversity (Bastolla et al. 2009). New studies introduced the idea that networks can vary from one locality to another. They can be meaningfully compared, either to understand the importance of environmental gradients on the presence of ecological interactions (Tylianakis et al. 2007), or to understand the mechanisms behind variation itself (Poisot et al. 2012, 2014).

Yet, meta-analyses of a large number of ecological networks are still extremely rare, and most of the studies comparing several networks do so within the limit of particular systems (Schleuning et al. 2011; Dalsgaard et al. 2013; Poisot et al. 2013b; Chamberlain et al. 2014; Olito & Fox 2014). The severe shortage of publicly shared data in the field also restricts the scope of large-scale analyses.

It is possible to predict the structure of ecological networks, either using latent variables (Rohr et al. 2010; Eklöf et al. 2013) or actual trait values (Gravel et al. 2013). The calibration of these approaches require accessible data, not only about the interactions, but about the traits of the species involved. Comparing the efficiency of different methods is also facilitated if there is an homogeneous way of representing ecological interactions, and the associated metadata. In this paper, we (i) establish the need of a data specification serving as a common language among network ecologists, (ii) describe this data specification, and (iii) describe \texttt{rmangal}, a R package and companion database relying on this data specification. The \texttt{rmangal} package allows to easily deposit and retrieve data about ecological interactions and networks in a publicly accessible database. We provide use cases showing how this new approach makes complex analyzes simpler, and allows for the integration of new tools to manipulate biodiversity resources.

Networks need a data specification

Ecological networks are (often) stored as an adjacency matrix (or as the quantitative link matrix), that is a series of 0 and 1 indicating, respectively, the absence and presence of an interaction. This format is extremely convenient for use (as most network analysis packages, \textit{e.g.} \texttt{bipartite}, \texttt{betalink}, \texttt{foodweb}, require data to be presented this way), but is extremely inefficient at storing meta-data (this can be done by adding attributes to the matrix objects in the language that support it). In most cases, an adjacency matrix informs on the identity of species (in cases where rows and columns are named), and the presence or absence of interactions. If other data about the environment (\textit{e.g.} where the network was sampled) or the species (\textit{e.g.} the population size, trait distribution, or other observations) are available, they are most either given in other files, or as accompanying text. In both cases, making a programmatic link between interaction data and relevant meta-data is difficult, time-consuming, and error-prone. Because of the lack of a common structure for these data, the process cannot be automated when different datasets needs to be processed.

By contrast, a data specification (\textit{i.e.} a set of precise instructions detailing how each object should be represented) provides a common language for network ecologists to interact, and ensure that, regardless of their source, data can be used in a shared workflow. Most importantly, a data specification describes how data are exchanged. Each group retains the ability to store the data in the format that is most convenient for in-house use, and only needs to provide export options (\textit{e.g.} through an API, a programmatic interface running on a webserver, returning data in response to queries in a pre-
determined language) respecting the data specification. This approach ensures that all data can be used in meta-analyses, thus increasing their long-term impact (Piwowar & Vision 2013). Data archival also offers additional advantages for ecology. The aggregation of local observation can reveal large-scale phenomenon (Reichman et al. 2011), which would be unattainable in the absence of a collaborative effort. Data archival in databases also prevents data rot and data loss (Vines et al. 2014), thus ensuring that data on interaction networks – which are typically hard and costly to produce – continue to be available and usable.

Elements of the data specification

The data specification (Fig. 1) is built around the idea that (ecological) networks are collections of relationships between ecological objects, each element having particular meta-data associated. In this section, we detail the way networks are represented in the mangal specification. An interactive webpage with the complete data specification can be found online at http://mangal.uqar.ca./doc/spec/. The data specification is available either at the API root (e.g. http://mangal.uqar.ca/api/v1/?format=json), or can be viewed using the whatIs function from the R package (see Supp. Mat. 1). Rather than giving an exhaustive list of the data specification, this section serves as an overview of each element, and how they interact.

We propose JSON as an efficient way to uniformise data representation for two main reasons. First, it has emerged as a de facto standard for web platforms serving data, and accepting data from users. Second, it allows validation of the data: a JSON file can be matched against a scheme, and one can verify that it is correctly formatted. Finally, JSON objects representing individual items are easily and cheaply (memory-wise) parsed in the most common programming languages, notably R (equivalent to list) and python (equivalent to dict). For most users, the format in which data are transmitted is unimportant, as the interaction happens within R – as such, knowing how JSON objects are organized is only useful for those who want to interact with the API directly. The rmangal package takes care of converting the data into the correct JSON format to upload them in the database.
Node information

Taxa

Taxa are a taxonomic entity of any level, identified by their name, vernacular name, and their identifiers in a variety of taxonomic services. Associating the identifiers of each taxa allows using the new generation of open data tools, such as taxize (Chamberlain & Szöcs 2013), in addition to protecting the database against taxonomic revisions. The data specification currently has fields for ncbi (National Center for Biotechnology Information), gbif (Global Biodiversity Information Facility), tsn (Taxonomic Serial Number, used by the Integrated Taxonomic Information System), eol (Encyclopedia of Life) and bold (Barcode of Life) identifiers. We also provide the taxonomic status, i.e. whether a taxa is a true taxonomic entity, a “trophic species”, or a morphospecies. Taxonomic identifiers can either be added by the contributors, or will be automatically retrieved during the automated curation routine.

Item

An item is any measured instance of a taxon. Items have a level argument, which can be either individual or population; this allows to represent both individual-level networks (i.e. there are as many items of a given taxa as there were individuals of this sampled), and population-level networks. When item represents a population, it is possible to give a measure of the size of this population. The notion of item is particularly useful for time-replicated designs: each observation of a population at a time-point is an item with associated trait values, and possibly population size.

Network information

All objects described in this sub-section can have a spatial position, information on the date of sampling, and references to both papers and datasets.

Interaction

An interaction links two taxa objects (but can also link pairs of items). The most important attributes of interactions are the type of interaction (of which we provide a list of possible values, see Supp. Mat. 1), and its ob_type, i.e. how it was observed. This field help differentiate direct observations, text mining, and inference. Note that the obs_type field can also take confirmed absence as a value; this is useful for, e.g., “cafeteria” experiments in which there is high confidence that the interaction did not happen.

Network

A network is a series of interaction object, along with (i) informations on its spatial position (provided at the latitude and longitude), (ii) the date of sampling, and (iii) references to measures of environmental conditions.

Dataset

A dataset is a collection of one or several network(s). Datasets also have a field for data and papers, both of which are references to bibliographic or web resources describing, respectively, the source of the data, and the papers in which
these data have been significantly used. Datasets or networks are the preferred entry point into the resources, although in some cases it can be meaningful to get a list of interactions only.

**Meta-data**

**Trait value**

Objects of type *item* can have associated *trait* values. These consist in the description of the trait being measured, the value, and the units in which the measure was taken. As traits may have been measured at a different time and/or location that the interaction was, they have fields for time, latitude and longitude, and references to original publication and original datasets.

**Environmental condition**

Environmental conditions are associated to datasets, networks, and interactions objects, to allow for both macro and micro environmental conditions. These are defined by the environmental property measured, its value, and the units. Similarly to traits, they have fields for time, latitude and longitude, and references to original publication and original datasets.

**References**

References are associated to datasets. They accommodate the DOI, JSON or PubMed identifiers, or a URL. When possible, the DOI should be preferred as it offers more potential to interact with other on-line tools, such as the CrossRef API.

**Use cases**

In this section, we present use cases using the *rmangal* package for R, to interact with a database implementing this data specification, and serving data through an API (http://mangal.uqar.ca/api/v1/). It is possible for users to deposit data into this database, through the R package. Data are made available under a *CC-0 Waiver* (Poisot *et al*. 2013a). Detailed informations about how to upload data are given in the vignettes and manual of the *rmangal* package.

The data we use for this example come from Ricciardi *et al*. (2010). These were previously available on the Interaction-Web Database as a single *xls* file. We uploaded them in the *mangal* database at http://mangal.uqar.ca/api/v1/dataset/1.

Before running the examples, users need to install the relevant packages and connect to the database:

**Link-species relationships**

In the first example, we visualize the relationship between the number of species and the number of interactions, which Martinez (1992) proposed to be linear (in food webs).

```r
# Pull the dataset of interest
dataset <- getDataset(api, DSET_ID)
```
# Get each network in the dataset as a graph object
graphs <- alply(dataset$networks, 1, function(x) toIgraph(api, x))

# Make a data.frame with the number of links and species
ls <- ldply(graphs, function(x) c(S = length(V(x)), L = length(E(x))))
ls$X1 <- aapply(as.numeric(as.vector(ls$X1)), 1, function(x) getNetwork(api, x)$name)
colnames(ls)[1] <- 'Network'

# Now plot this dataset
plot(jitter(L)~jitter(S), ls, log='xy', pch=22, bg='lightgrey',
     lwd=1.5, cex=1.5, xlab='Species richness', ylab='Number of interactions')

# Constant connectance
X <- c(1:max(ls$S))
Y <- X^2 * mean(ls$L/ls$S^2)
lines(X, Y, lty=2)

# Best fit
bfit <- lm(L~S, ls)
lines(X, Yf)

legend('bottomright', pch=c(22, NA, NA), lty=c(NA, 2, 1),
       pt.cex=c(1.5, 1, 1), lwd=c(1.5, 1, 1), pt.bg=c('lightgrey', NA, NA),
       legend=c('Data', 'Constant connectance', 'Best fit (linear model)'), bty='n')

Getting the data to produce Fig. 2 requires less than 10 lines of code. The only information needed is the identifier of the network or dataset, which we suggest should be reported in publications as: “These data were deposited in the mangal format at <URL>/api/v1/dataset/<ID>” (where <URL> and <ID> are replaced by the corresponding values), preferably in the methods, possibly in the acknowledgements. So as to encourage data sharing and its recognition, we encourage users of the database to cite the original dataset or publication.

Network beta-diversity

In the second example, we use the framework of network $\beta$-diversity (Poisot et al. 2012) to measure the extent to which networks that are far apart in space have different interactions. Each network in the dataset has a latitude and longitude, meaning that it is possible to measure the geographic distance between two networks.

For each pair of network, we measure the geographic distance (in km.), the species dissimilarity ($\beta_S$), the network dissimilarity when all species are present ($\beta_{WN}$), and finally, the network dissimilarity when only shared species are considered ($\beta_{OS}$).

# We first retrieve all informations about the networks
Networks <- alply(dataset$networks, 1, function(x) getNetwork(api, x))

# Extract the lat/lon data
Fig. 2: Relationship between the number of species and number of interactions in the anemonefish-fish dataset. Constant connectance refers to the hypothesis that there exist a quadratic relationship between these two quantities.
LatLon <- ldply(Networks, function(x) c(name = x$name, lat = x$latitude, lon = x$longitude))
rownames(LatLon) <- LatLon$name
LatLon$lat <- as.numeric(LatLon$lat)
LatLon$lon <- as.numeric(LatLon$lon)
LatLon <- LatLon[,c('lat', 'lon')]

# Then we measure the distances between all pairs of sites
GeoDist <- spDists(as.matrix(LatLon, latlon=TRUE))
colnames(GeoDist) <- rownames(GeoDist) <- rownames(LatLon)
GeoDist <- as.dist(GeoDist)

# Now, we measure the beta-diversity of the networks
names(graphs) <- apply(names(graphs), 1, function(x) Networks[[x]]$name)
# Finally, we measure the beta-diversity
BetaDiv <- network_betadiversity(graphs)

# We add the geographic distance
BetaDiv$GEO <- GeoDist

# And we do some plots
par(mfrow=c(2,2), pty='s')
with(BetaDiv, {
  plot(GEO, S, pch=22, bg='lightgrey', cex=1.5, lwd=1.5,
       xlab="Geographic distance", ylab="Species composition dissimilarity")
  plot(GEO, WN, pch=22, bg='lightgrey', cex=1.5, lwd=1.5,
       xlab="Geographic distance", ylab="Network dissimilarity (all species)")
  plot(GEO, OS, pch=22, bg='lightgrey', cex=1.5, lwd=1.5,
       xlab="Geographic distance", ylab="Network dissimilarity (shared species)")
})

As shown in Fig. 3, while species dissimilarity and overall network dissimilarity increase when two networks are far apart, this is not the case for the way common species interact. This suggests that in this system, network dissimilarity over space is primarily driven by species turnover. The ease to gather both raw interaction data and associated meta-data make producing this analysis extremely straightforward.

Spatial visualization of networks

Bascompte (2009) uses an interesting visualization for spatial networks, in which each species is laid out on a map at the center of mass of its distribution; interactions are then drawn between species to show how species distribution determines biotic interactions. In this final use case, we propose to reproduce a similar figure (Fig. 4).

# We fill a community data matrix
sp_by_site <- llply(graphs, function(x) unlist(V(x)$name))
Fig. 3: Relationships between the geographic distance between two sites, and the species dissimilarity, network dissimilarity with all, and only shared, species.
sp_list <- unique(unlist(sp_by_site))
M <- matrix(0, ncol = length(sp_list), nrow = length(sp_by_site))
colnames(M) <- sp_list
rownames(M) <- names(sp_by_site)
for (site in c(1:length(sp_by_site))) M[names(sp_by_site)[site], sp_by_site[[site]]] = 1

# Next, we get the center position for each species
# (i.e. the mean position of the sites it occurs at)
sp_center <- adply(M, 2, function(x) col Means(LatLon[names(x)[x > 0], ]))
rownames(sp_center) <- sp_center[, 1]
sp_center <- sp_center[, -1]

# We now create a regional network using betalink::metaweb
Mw <- metaweb(graphs)

# Plot a map
center_point <- colMeans(sp_center)
vcolors <- c(brewer.pal(9, "Set1"), brewer.pal(8, "Set2"))

Layout <- matrix(c(1, 2, 2, 2), 2, 2)
colSize <- c(1.3, 2.0)
rowSize <- c(1.2, 2)
layout(Layout, colSize, rowSize)

# Inset map is number 1
par(mar=c(4.5, 1, 1, 4))
map("worldHires", xlim=c(90, 136), ylim=c(-15, 15), col="gray90",
    fill=TRUE, resolution=0)
points(center_point[2], center_point[1], pch=1, cex=2, lwd=2)
box()
par(mar=c(4.1, 4.1, 4.1, 4.1))
map("worldHires", xlim=c(124.0, 125.1), ylim=c(1.2, 1.9), col="gray90",
    fill=TRUE, resolution=0)
plot(Mw, layout = jitter(as.matrix(LatLon[, c('lon', 'lat')])),
    rescale = FALSE, add = TRUE, vertex.color = vcolors, vertex.size = 1,
    vertex.label = NA, edge.arrow.size = 0.25, edge.color = 1)
axis(1)
axis(4)
legend("bottomleft", fill = vcolors, legend = V(Mw)$name, inset = 0.02,
    cex = 0.7, bty = "n", ncol=2)
Fig. 4: Spatial plot of a network, using the \texttt{maps} and \texttt{rmapal} packages. The circle in the inset map show the location of the sites. Each dot in the main map represents a species, with (symbiotic mutualism) drawn between them. The land is in greyscale.
Conclusions

The mangal data format will allow researchers to put together dataset with species interactions and rich meta-data, that are needed to address emerging questions about the structure of ecological networks. We deployed an online database with an associated API, relying on this data specification. Finally, we introduced rmangal, a R package designed to interact with APIs using the mangal format. We expect that the data specification will evolve based on the needs and feedback of the community. At the moment, users are welcome to propose such changes on the project issue page: https://github.com/mangal-wg/mangal-schemes/issues. A python wrapper for the API is also available at http://github.com/mangal-wg/pymangal/. Additionally, there are plans to integrate this database with GLOBI, so that data can be accessed from multiple sources (Poelen et al. 2014).

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References


