

Environmental biases in the study of ecological networks at the planetary scale

Introduction

Ecological networks are a useful way to think about ecological systems in which species or organisms interact (Heleno et al. 2014; Poisot et al. 2016c; Delmas et al. 2018), and recently there has been an explosion of interest in their dynamics across large temporal scales (Tylianakis & Morris 2017; Baiser et al. 2019), and especially along environmental gradients (Trøjelsgaard & Olesen 2016; Pellissier et al. 2017). As ecosystems and climates are changing rapidly, networks are at risk of unravelling: for example by invasion of destabilizing exotic species them (Strong & Leroux 2014; Magrath et al. 2017), or by a “rewiring” of interactions among existing species (Guiden et al. 2019; Hui & Richardson 2019). Simulation studies suggest that knowing the shape of the extant network is not sufficient (Thompson & Gonzalez 2017), and that it needs to be supplemented by additional data on the species in the food web, climate, and climate projection.

This renewed interest in ecological networks has prompted several methodological efforts. First, an expansion of the analytical tools to study ecological networks and their variation in space (Poisot et al. 2012, 2015, 2017). Second, an improvement in large-scale data-collection, through increased adoption of molecular biology tools (Evans et al. 2016; Eitzinger et al. 2019) and crowd-sourcing of data collection (Pocock et al. 2015; Bahlai & Landis 2016; Roy et al. 2016). Finally, a surge in the development of tools that allow us to *infer* species interactions (Morales-Castilla et al. 2015) based on limited but complementary data on existing network properties (Stock et al. 2017), species traits (Gravel et al. 2013; Desjardins-Proulx et al. 2017; Brousseau et al. 2017; Bartomeus et al. 2016), and environmental conditions (Gravel et al. 2018). These latter approaches tend to perform well in data-poor environments (Beauchesne et al. 2016), and can be combined through ensemble modeling or model averaging to generate more robust predictions (Pomeranz et al. 2018). The task of inferring interactions is particularly important because ecological networks are difficult to adequately sample in nature (Banašek-Richter et al. 2004; Gibson et al. 2011; Chacoff et al. 2012; Jordano 2016). The common goal to these efforts is to facilitate the prediction of network structure, particularly over space [Poisot

et al. (2016b); Gravel et al. (2018); (tk) Albouy et al Nat Ecol Evol 2018] and into the future (Albouy et al. 2014), and to appraise the response of that structure to possible environmental changes.

These disparate methodological efforts share another important trait: their continued success depends on state-of-the art data management. Novel quantitative tools demand a higher volume of network data; novel collection techniques demand powerful data repositories; novel inference tools demand easier integration between different types of data, including but not limited to: interactions, species traits, taxonomy, occurrences, and local bioclimatic conditions. In short, advancing the science of ecological networks requires us not only to increase the volume of available data, but to pair these data with ecologically relevant metadata. Such data should also be made available in a way that facilitates programmatic interaction so that they can be used by reproducible data analysis pipelines.

Poisot et al. (2016a) introduced `mangal.io` as a first step in this direction. In the years since the tool was originally published, we continued development of the data representation, amount and richness of metadata, and digitized and standardized as much ecological data as we could find. The second major release of this database contains over 1300 networks, 120000 interactions across close to 7000 taxa, and represents what is to our best knowledge the most complete collection of species interactions available.

Here we ask if the current mangal database is fit for the purpose of global-scale synthesis research into ecological networks. We conclude that interactions over most of the planet’s surface are poorly described, despite an increasing amount of available data, due to temporal and spatial biases in data collection. In particular, Africa, South America, and most of Asia have very sparse coverage. This suggests that synthesis efforts on the worldwide structure or properties of ecological networks will be weaker within these areas. To improve this situation, we should digitize available network information and prioritize sampling towards data-poor locations.

Global trends in ecological networks description

Network coverage is accelerating but spatially biased

The earliest recorded ecological networks date back to the late nineteenth century, with a strong increase in the rate of collection around the 1980s (fig. 1). Although the volume of available networks has increased over time, the sampling of these networks in space has been uneven. In fig. 2, we show that globally, network collection is biased towards the Northern hemisphere, and than different types of interactions have been sampled in different places. As such, it is very difficult to find a spatial area of sufficiently large size in which we have

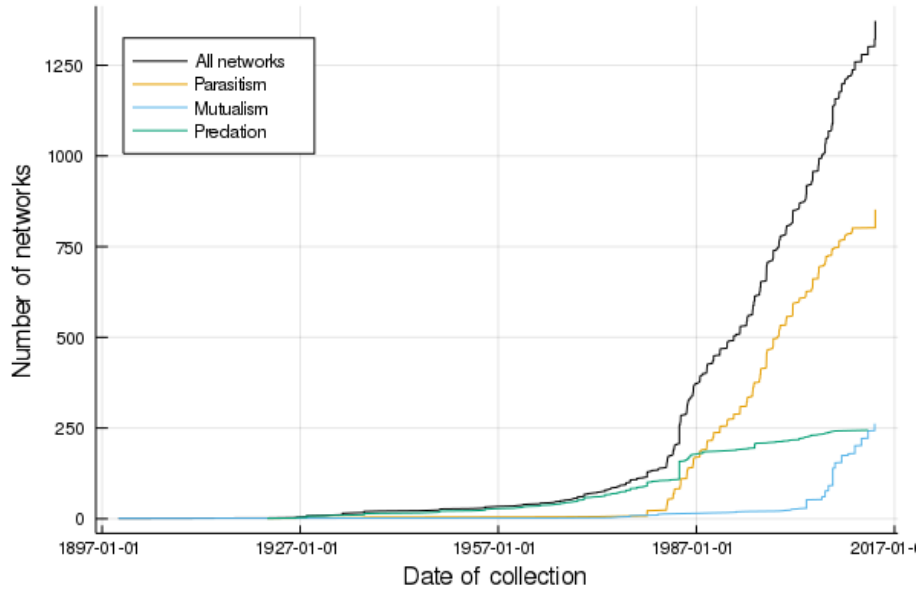


Figure 1: Cumulative number of ecological networks available in `mangal.io` as a function of the date of collection. About 1000 unique networks have been collected between 1987 and 2017, a rate of just over 30 networks a year. This temporal increase proceeds at different rates for different types of networks; while the description of food webs is more or less constant, the global acceleration in the dataset is due to increased interest in host-parasite interactions starting in the late 1970s, while mutualistic networks mostly started being recorded in the early 2000s.

networks of predation, parasitism, and mutualism. The inter-tropical zone is particularly data-poor, either because data producers from the global South correctly perceive massive re-use of their data by Western world scientists as a form of scientific neo-colonialism (as advanced by Mauthner & Parry 2013), thereby providing a powerful incentive *against* their publication, or because ecological networks are subject to the same data deficit that is affecting all fields on ecology in the tropics (Collen et al. 2008). As Bruna (2010) identified almost ten years ago, improved data deposition requires an infrastructure to ensure they can be repurposed for future research, which we argue is provided by `mangal.io` for ecological interactions.

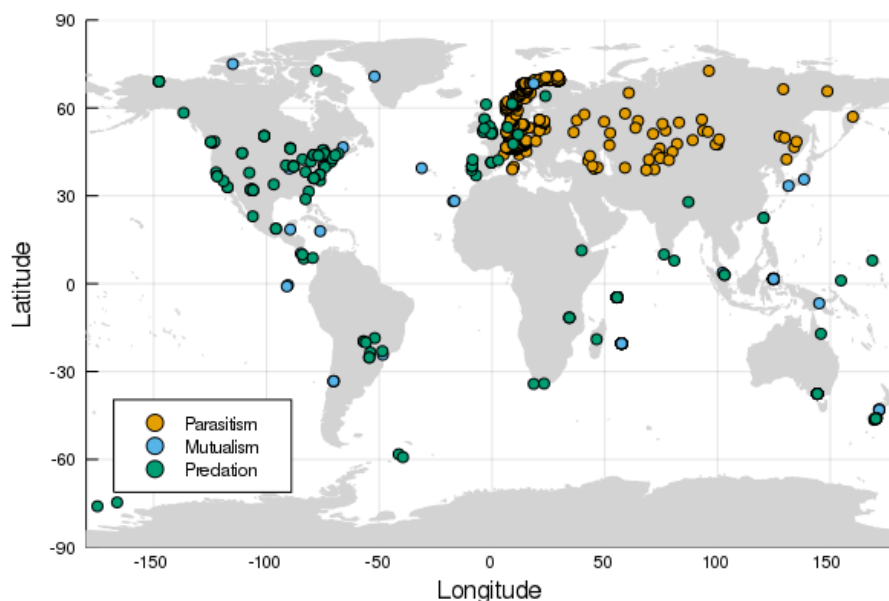


Figure 2: Each point on the map corresponds to a network with parasitic, mutualistic, and predatory interactions. It is noteworthy that the spatial coverage of these types of interactions is uneven; the Americas have almost no parasitic network, for example. Some places have barely been studied at all, including Africa and Eastern Asia. This concentration of networks around rich countries speaks to an inadequate coverage of the diversity of landscapes on Earth.

Different interaction types have been studied in different biomes

Whittaker (1962) suggested that natural communities can be partitioned across biomes, largely defined as a function of their relative precipitation and temperature. For all networks for which the latitude and longitude was known, we

extracted the value temperature (BioClim1, yearly average) and precipitation (BioClim12, total annual) from the WorldClim 2 data (Fick & Hijmans 2017). Using these we can plot every network on the map of biomes drawn by Whittaker (1962) (note that because the frontiers between biomes are not based on any empirical or systematic process, they have been omitted from this analysis). In fig. 3, we show that even though networks capture the overall diversity of precipitation and temperature, types of networks have been studied in sub-spaces only. Specifically, parasitism networks have been studied in colder and drier climates; mutualism networks in wetter climates; predation networks display less of a bias.

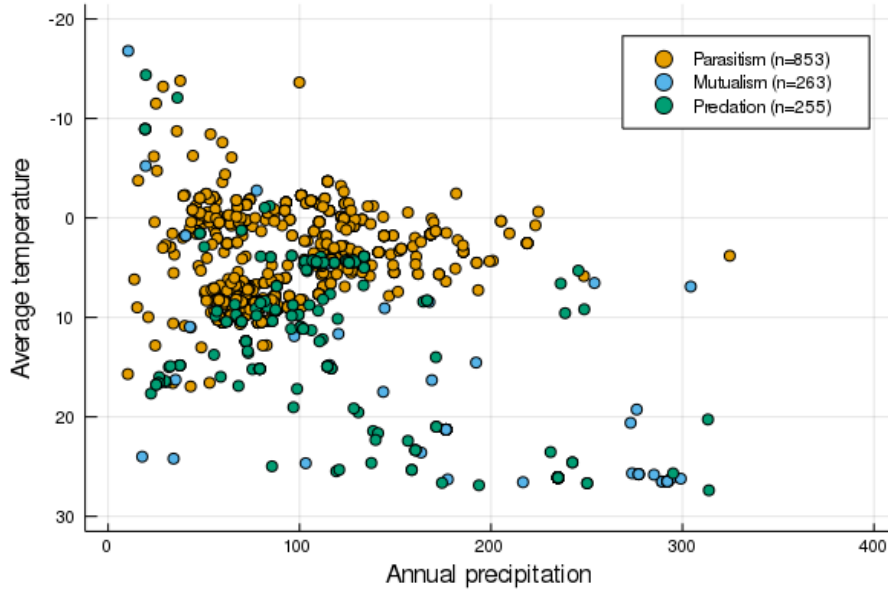


Figure 3: List of networks across in the space of biomes as originally presented by Whittaker (1962). Predation networks, *i.e.* food webs, seem to have the most global coverage; parasitism networks are restricted to low temperature and low precipitation biomes, congruent with the majority of them being in Western Europe.

Scaling up this analysis to the 19 BioClim variables in Fick & Hijmans (2017), we extracted the position of every network in the bioclimatic space, conducted a principal component analysis on the scaled bioclimatic variables, and measured their distance to the centre of this space ($\mathbf{0}$). This is a measurement of the “rarity” of the bioclimatic conditions in which any networks were sampled, with larger values indicating more unique combinations (the distance was ranged to $]0;1]$ for the sake of interpretation). As shown in fig. 4, mutualistic interactions tend to have values that are higher than both parasitism and predation, suggesting that they have been sampled in more unique environments.

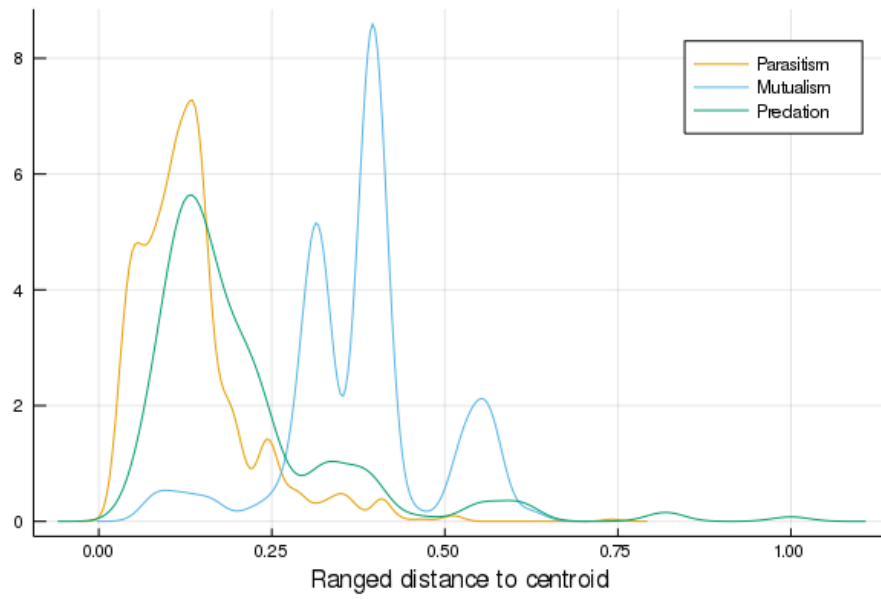
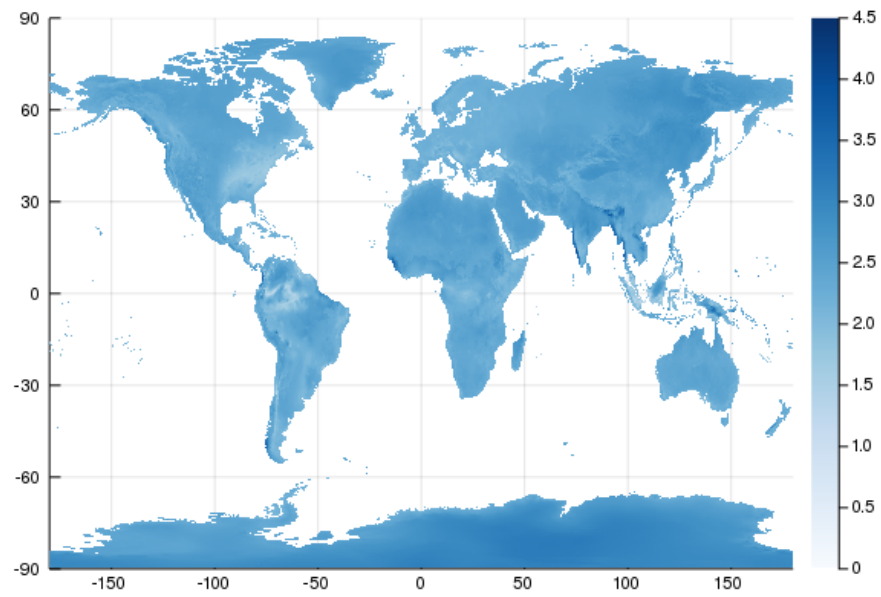
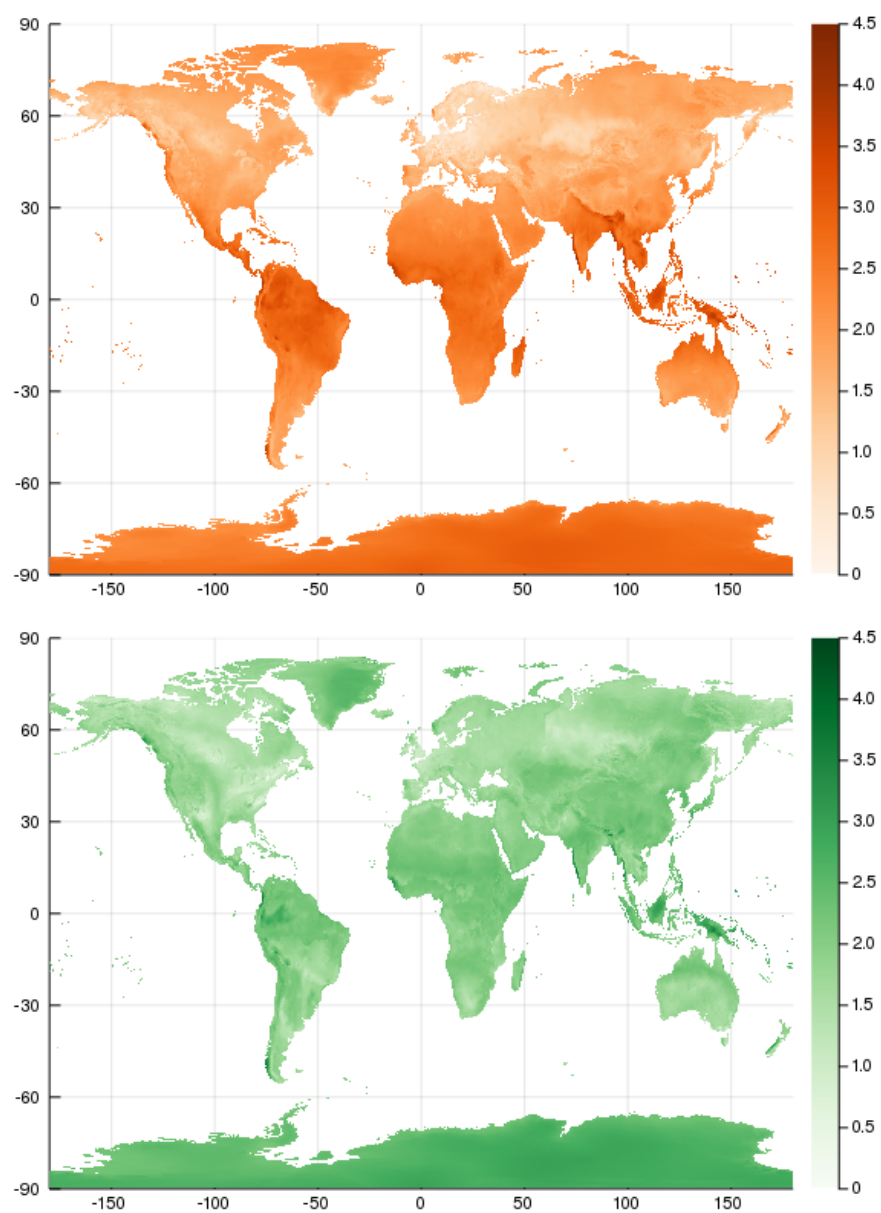


Figure 4: tk

Some locations on Earth have no climate analogue

Climate analogue





Conclusions

Can we predict the future of ecological networks under climate change?

Perhaps unsurprisingly, most of our knowledge on ecological networks is derived from data that were collected after the 1990s (fig. 1). This means that we have worryingly little information on ecological networks before the acceleration of the climate crisis, and therefore lack a robust baseline. Dalsgaard et al. (2013) provide strong evidence that the extant shape of ecological networks emerged in part in response to historical trends in climate change. The lack of reference data before the acceleration of the effects of climate change is of particular concern, as we may be deriving intuitions on ecological network structure and assembly rules from networks that are in the midst of important ecological disturbances. Although there is some research on the response of co-occurrence and indirect interactions to climate change (Araújo et al. 2011; Losapio & Schöb 2017), these are a far cry from actual direct interactions; similarly, the data on “paleo-foodwebs”, *i.e.* from deep evolutionary time (Nenzén et al. 2014; Yeakel et al. 2014; Muscente et al. 2018) represent the effect of more progressive change, and may not adequately inform us about the future of ecological networks under severe climate change. However, though we lack baselines against which to measure the present, as a community we are in a position to provide one for the future. Climate change will continue to have important impacts on species distributions and interactions for at least the next century [tk]. The Mangal database provides a structure to organize and share network data, creating a baseline for future attempts to monitor and adapt to biodiversity change.

Possibly more concerning is the fact that the spatial distribution of sampled networks shows a clear bias towards the Western world, specifically Western Europe and the Atlantic coasts of the USA and Canada (fig. 2). This problem can be somewhat circumvented by working on networks sampled in places that are close analogues of those without direct information (almost all of Africa, most of South America, a large part of Asia). However, (???) suggests that this approach will rapidly be limited: the diversity of bioclimatic combinations on Earth leaves us with some areas lacking suitable analogues. These regions are expected to bear the worst of the socio-economical (*e.g.* Indonesia) or ecological (*e.g.* polar regions) consequences of climate change [tk]. All things considered, our current knowledge about the structure of ecological networks at the global scale leaves us under-prepared to predict their response to a warming world.

For what purpose are global ecological network data fit?

What can we achieve with our current knowledge of ecological networks? The overview presented here shows a large and detailed dataset, compiled from almost every major biome on earth. It also displays our failure as a community

to include some of the most threatened and valuable habitats in our work. Gaps in any dataset create uncertainty when making predictions or suggesting causal relationships. This uncertainty must be measured by users of these data, especially when predicting over the “gaps” in space or climate that we have identified. In this paper we are not making any explicit recommendations for synthesis workflows. Rather we think this needs to be a collective process, a collaboration between data collectors (who understand the deficiencies of these data) and data analysts (who understand the needs and assumptions of network methods).

One possible avenue for synthesis work, including the contribution of new data to Mangal, is the use of these published data to supplement and extend existing ecological network data. This “semi-private” ecological synthesis could begin with new data collected by authors – for example, a host-parasite network of lake fish in Africa, or a pollination network of hummingbirds in Brazil. Authors could then extend their analyses by including a comparison to analogous data made public in Mangal. After publication of the research paper, the original data could themselves be uploaded to Mangal. This enables the reproducibility of this particular published paper. Even more powerfully, it allows us to build a future of dynamic ecological analyses, wherein analyses are automatically re-done as more data get added. This would allow a sort of continuous assessment of proposed ecological relationships in network structure. This cycle of data discovery and reuse is an example of the Data Life Cycle (as discussed by DataOne, [tk]) and represents one way to practice ecological synthesis.

Active development and data contribution

This is an open-source project: all data and all code supporting this are available on the Mangal project GitHub organization. Our hope is that the success of this project will encourage similar efforts within other parts of the ecological community. In addition, we hope that this project will encourage the recognition of the contribution that software creators make to ecological research.

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