# Biogeography of Parasites

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"Essentially, all models are wrong, but some are useful." - George Box

New Introduction structure

Paragraph themes:

* Climate change is going to have immense consequences on the biotic world
  + List measured changes within the ocean
  + See if there are species adapting … and species that aren’t as examples
* What have climate models predicted for marine species.
* But many of these predictions are only on free-living species and don’t consider the hidden biodiversity… parasites
* There has been research on parasite risk to changes in climate … but …
  + Most are on land
  + Speaking about “coextinction risk” and a growing body of theoretical work on potential impacts… there hasn’t been much in the line of predictions…
  + This is probably due to a lack of long term data required to detect extinctions in progress.
* Speak about the imperative role that parasites play in ecosystems and that if there is a change in their distribution/ extinction … it could have cascading effects on ecosystem functioning.
  + For example changes in distribution could negatively effect food stocks farms etc.
  + And if extinction happens it could change how ecosystems function for the negative … spell it out.
* Aims and objectives…

(Carlson *et al.*, 2017) use this as a template and as a reference list.

Biogeography is a top-down view of the distribution of organisms through geological time and aims to record and understand these spatial variations across environments (Lomolino *et al.*, 2010). The term came into existence in the 1800’s as advances in technology allowed biologists and naturalists to travel to the far reaches of our planet; documenting, collecting and describing the various plants and animals they stumbled across. Over the years, the field has expanded and refined our understanding of the global distribution of species due to an understanding of continental movement; improved methods for molecular systematics; and has advanced our ability to compile, visualize, and analyse geographic information (Lomolino *et al.*, 2010).

One of the fundamental components of biogeography is documenting the biodiversity of a region or ecosystem. Knowing what species occur within an ecosystem and understanding the role these species play, allows ecologists to understand how an ecosystem functions. With new species being discovered almost daily (e.g.: Hug et al. 2016), finding and describing the number of species that occurs is a herculean task. Increasing evidence indicates that two thirds of species on Earth have already been named (Costello and Chaudhary, 2017), with researchers predicting that most of the remaining species will be named by 2100 (Costello, May and Stork, 2013).

Yet, there are many inconsistencies with these predictions. Costello and Chaudhary (2017) identify and discuss many of these problems. They speak about the significance of unrecognised synonyms, the potential hyper-diversity of microbes, parasites, and deep sea species, and the relationship of molecular (cryptic) diversity to new species. Completing our knowledge of biodiversity will assist in biogeographical studies and provide environmental researchers and managers a yard stick to measure the catastrophic impact of climate change on global biodiversity (Costello, May and Stork, 2013).

## Parasites

“Parasitism, including parasitism in the oceans, is almost as old as life itself” - (Rohde, 2002)

Parasites are found in almost all taxa of eukaryotes, evolving independently at least 223 times across 15 phyla (Weinstein and Kuris, 2016). Yet, the role of parasites in ecosystem functioning has been considered trivial, as historical examinations reveal that their relative biomass is low compared with that of other trophic groups (Hudson, Dobson and Lafferty, 2006). These parasitic animals are small, short-lived and rarely observed in the external environment and during their parasitic phase, are more commonly hidden within or on their hosts.

However, there is growing evidence indicating that as parasite diversity increases, there is a marked improvement in ecosystem functioning (Preston et al., 2016). Therefore, how can we expect these reprehensible citizens to have the capabilities to engineer ecosystems if their functioning within an ecosystem is considered ‘trivial’?

Researchers have followed the impacts of parasites on ecosystems by measuring the effects they have on their hosts (Hudson, Dobson and Lafferty, 2006). These organisms have evolved to cope with and fend off their host’s defences; in some cases affecting the morphology and appearance of their host, and changing their host’s behaviour to further their own life history goals (Marcogliese, 2004). These strategies have allowed these animals to modulate how energy flows through ecosystems by changing predator-prey interactions; modifying food web dynamics and, as a result, altering community structure (Thomas and Poulin, 1998; Thomas *et al.*, 1998; Lafferty, 2008). These adaptations provide the key to understand just how important these organisms are in structuring ecosystems.

Ecologists admit that there is still much work that needs to be conducted on parasites, even for well-known marine host animals such as seabirds. It is predicted that half of all biodiversity might comprise of parasitic species (Toft, 1986), with parasitism evolving in 15 of the 35 recognised phyla (± 40%) (Weinstein and Kuris, 2016), yet of described species, parasites of animals comprise only 5% (Costello, 2016). Rohde (2002) provides considerations with respect to why there is this disparity in parasite numbers and that rough estimates of the richness of most parasite groups in the oceans are premature for the following reasons:

* Species numbers of host groups, in particular in the deep sea and the meiofauna, are not known;
* Most host groups have been examined only insufficiently for parasites or not at all;
* Even in some of the best known groups, latitudinal, longitudinal and depth gradients in species richness are only poorly understood or not known at all;
* Effects of hosts on parasite morphology and geographical variation have been studied only in a few cases;

Specifically:

* Parasites are smaller than their host and are often concealed within their host. This makes finding and studying them very difficult.
* There are a lack of surveys particularly with the objective of locating and identifying parasitic species, with particular reference to a lack of taxonomic surveys involving molecular analysis
* The empirical rule, Body-Size relation (May 1990) seems to fall apart under 1cm, making predictions more difficult
* Synonymy between species, particularly in well studies clades

Various methods from ecology have been adapted, altered, and used to understand what drives parasitic community structure, with the aim of gaining a brief glimpse into this cryptic lifestyle. Many of these methods have come from the biogeographical realm and are discussed below. Unfortunately, the general trend in utilizing these methods is that it provides more questions than answers but such is scientific endeavour :)

## Parasites in biogeography

### Island biogeography

Island biogeography provides elegant examples of the evolutionary mechanisms involved in generating biodiversity, and is equally relevant in parasite biogeography (Kuris, Blaustein and Alio, 1980). Island biogeography proposes that the number of species found in an isolated environment (or island) is determined by immigration and extinction (Macarthur and Wilson, 1963). And further, that the isolated populations may follow different evolutionary routes, as shown by Darwin's observation of finches in the Galapagos Islands. Immigration and emigration are affected by the distance of an island from a source of colonists, this is called a ‘distance effect’. Usually this source is the mainland, but it can also be other islands. Islands that are isolated are less likely to receive immigrants than islands that are more accessible.

Island biogeography theory has demonstrated its value in understanding the dynamics that impact isolated communities, not just islands themselves, but isolated habitat units in general (Kuris, Blaustein and Alio, 1980; Poulin, Krasnov, *et al.*, 2011). Jazen (1968) mentioned the use of plants as ‘islands’ for insects that feed on them and this piqued the interest of parasitologists, in that hosts could be treated as islands (on an individual, species, or population level). Kuris et al. (1980) reviewed much of this early work and cautioned the use of island biogeography theories being used on parasite-host systems, due to differences between moving hosts and stationary islands; particularly considering differences in microhabitat diversity, physiological and morphological variability of hosts and their parasites, and the link created through the coevolution of parasite and hosts (phylogenetics).

### Phylogenetics

Ecologists working on free-living communities have traditionally assumed that communities that are geographically distant represent statistically independent observations. For instance, the origin and history of an island in the Pacific Ocean is independent from the origin and history of an island in the Atlantic; one can examine the effects of variables such as island area or distance from continents on their communities without worrying about the "ancestry" of the islands. However, current literature in this field has begun realizing the effect of phylogenetics (Heaney, 2007); understanding the co-evolutionary relationship among populations and species and how they relate to the geological history of islands.

Parasite communities have provided an interesting method in testing the effect of phylogenetics on island communities: their habitats, like islands, are genealogically linked. This is due to the uniqueness of the parasitic lifestyle. For most of the parasites life, they depend on their hosts for essential resources; particularly food and shelter. This has implications for parasite spatial ecology as their distribution is almost solely controlled by their hosts (Krasnov *et al.*, 2004). This exclusivity for hosts has implications for how traits between hosts and parasites are lost or conserved over time and studies have shown the strong interconnectedness of traits through phylogenetic trees (Krasnov, Morand and Poulin, 2015). Therefore, phylogenetically based comparative methods can and have contributed to biogeographic research (Poulin, Krasnov, *et al.*, 2011).

### Species area relationships

Species area relationships (SARs) have assisted ecologists in distinguishing hotspots of biodiversity and provide a powerful tool to control for host body size within parasitology. The size of the host’s body is seen as an overall measure of habitat dimension, niche diversity and food supply and should also correlate with encounter rates. However, the predictive power of host body size has generally been very weak in past analyses (Poulin and Morand, 2000; Kamiya *et al.*, 2014). Poulin *et al.* (2011a) utilize SARs to show that host body size is an unsuccessful universal predictor of parasite species richness. The researchers conclude that exceptional parasite diversity (increased infection rates) shows a stronger association with host phylogeny than with host size and ecology.

### Species accumulation curves.

Species richness is a measurement central to the understanding of community and regional diversity (Gotelli and Colwell, 2001). It allows us to place a quantitative measurement on the comparisons between different sites within an ecosystem, and it is these comparisons that form the basis for community and conservation ecology. Studies of parasite diversity can benefit from the application of species richness measurements, as they provide information on the unseen biodiversity that ecosystems, and in the case of parasites, organisms may be hiding (Dove and Cribb, 2006).

Dove and Cribb (2006) recommends utilizing a method that has only recently been used in parasitic surveys, Species Accumulation Curves (SAC’s). SAC’s are useful in providing an estimate of the total number of species for a given host population and provides a measure of sampling effort. Properties of SAC’s are also incredibly informative of community patterns and the structure of parasitic and host diversity. Dove and Cribb warn that knowledge of the true distribution of parasite richness over multiple host-derived and spatial scales is far from complete but SACs can improve the understanding of diversity patterns in parasite and host assemblages.

### Interactive isolationist continuum

Holmes & Price (1986) first proposed the concept of an interactive–isolationist continuum of parasite community structure. It refers to parasitic infracommunities, which are the sub-populations of parasites living within individual hosts (Poulin, 2001). Dove & Cribb (2006) define interactive infracommunities as communities composed of species with high transmission rates, engaged in strong interspecific interactions, leading to predictable infracommunity structure and high similarity among infracommunities across the host population. Isolationist infracommunities, by contrast, are considered to be composed of species with low transmission rates, engaged in few or weak interspecific interactions, leading to unpredictable infracommunity structure and low similarity between infracommunities.

This method is predominantly used to determine the parasite community structure across a host population, and has been used to infer host community structure e.g. (Poulin and Luque, 2003). Poulin and Luque (2003) conclude that its application should provide researchers with a useful first approximation when determining what impact different types of hosts have on the nature of parasite communities.

### Latitudinal, longitudinal and environmental trends

Most groups of animals, whether terrestrial, freshwater or marine, show general changes in species numbers from high to low latitudes (Hillebrand, 2004; Chaudhary, Saeedi and Costello, 2016, 2017), along longitudinal gradients () and with various other geographical (e.g.: depth, altitude) and/or environmental (e.g.: precipitation, temperature) gradients. The increase of species diversity from the poles toward the tropics is the single most interesting pattern in biodiversity and the reasons for this pattern has fascinated ecologists for over a century (Pianka, 1966; Rohde, 1984, 2002; Hillebrand, 2004; Chaudhary, Saeedi and Costello, 2016).

Among marine parasites, latitudinal gradients in diversity with an increase in diversity towards the equator, have been shown for genera of Monogenea and Digenea (Rohde, 1984, 2002). However, these data have not been corrected for sampling bias (Chaudhary, Saeedi and Costello, 2017). Although several robust patterns have been revealed, studies that have corrected for these biases have shown we are far from achieving a clear understanding of the mechanisms behind the geographic variation of parasites (Guilhaumon *et al.*, 2012). Researchers have hypothesized that large-scale patterns in parasite richness should mirror those of their hosts, as parasites and their hosts are involved in intimate interactions. However, these researchers have revealed only weak and inconsistent evidence in favour of marine parasite latitudinal diversity gradients (Poulin and Morand, 2004).

Longitudinal gradients?

Depth gradients?

Statistical models? Such as: GAM’s ? GLMM ? (Jorge and Poulin, 2018)

(Poulin and Pérez-Ponce de León, 2017) - Global analysis reveals that cryptic diversity is linked with habitat but not mode of life

R.

### SDM’s

Scientific research refers to a particular method for acquiring knowledge about natural phenomena. This method has two dimensions: one of observation and experimentation and one of description and explanation. Sometimes, observation precedes explanation, and sometimes a proposed explanation precedes experimental confirmation. A scientific explanation is often made by creating a model of (some definable part of) reality. An advantage of general models is that they provide a hypothesis that can be falsified, whereas more limited data from limited observations may not be easily generalized (Costello *et al.*, 2017).

By estimating the relationships between species records at sites and the environmental and/or spatial characteristics of those sites, species distribution models (also known as “bioclimatic envelope models”, ‘‘ecological niche models’’ or ‘‘habitat suitability models’’) define sets of conditions under which species are likely to maintain viable populations (Elith *et al.*, 2011). Species distribution models (SDMs) have become commonplace in studies of biogeography, conservation biology, ecology, palaeo-ecology and wildlife management (Araújo and Guisan, 2006). In the last two decades, there have been many developments in the field of SDMs, and multiple methods are now available (Elith *et al.*, 2011).

SDMs are being used as a computational tool with multiple objectives; including discovery of new populations, discovery of previously unknown species, conservation planning, assessment of potential geographic ranges of invasive species, mapping risk of disease transmission, forecasting effects of climate change on species’ distributions and on phylogenetic diversity, and identifying historical refugia for biodiversity.chief amongst them being predicting the impacts of global climate change, especially global warming, on global and regional populations (Robinson et al., 2017). These predictions can be projected into either the past or the future, assuming that current climatic requirements of a species remain unchanged (Yates et al., 2010). However, being at the forefront of a data-centred paradigm shift (Kelling *et al.*, 2009), there are continued concerns surrounding this method (Text box x). Yet, As contentious as these methods may be, researchers in his field cannot deny the usefulness of these models.

Text box x: Over arching challenges identified by Araújo and Guisan (2006)

Araújo & Guisan (2006) identify some overarching challenges with species distribution modelling. Some of these include:

* Clarification of the niche concept

There are conflicting views about what the models truly represent. These conflicting interpretations arise from ambiguities in the original formulation of the niche concept formulated thorough Hutchinson’s realized vs. fundamental niche framework.

* Improved designs for sampling data used in building models

Model outputs are sensitive to sampling biases in the input data. Even though well-designed recording schemes are more likely to produce useful data for modelling, it is the poor quality of data that justifies the use of species’ distribution models in many applications.

* Improved parameterization strategies

Different parameterizations of the same model may yield considerably different projections of species potential habitats or distributions. The existence of variability in model outputs due to differences in model parameterization constitutes a form of uncertainty that has been previously underestimated.

* Improved model selection and predictor contribution

There are a number of relatively novel model selection strategies available that should be more widely used by ecological modellers.

* Improved model evaluation strategies

Evaluation of models is inextricably related to their intended purpose. Even though this seems a trivial statement, modellers often use model evaluation strategies without considering the object and goals of the modelling exercise.

Araújo & Guisan (2006) recommend deepening the debate on this incredibly useful tool and being cogniscent of their associated issues. Since the above publication, there has certainly been a deepening of the discussion as this approach to species-level biogeography and ecology now ranks among the most widely reviewed topics in the ecological literature (Araújo and Peterson, 2012). As contentious as this topic may be, researchers in his field cannot deny the usefulness of these models.

Take, for example, their use in predicting the emergence, spread and frequency of outbreaks of terrestrial human parasitic infections (e.g.: malaria, trypanosomiasis, schistosomiasis, onchocerciasis, and lymphatic filariasis) while keeping the unpredictability of changing climates in mind (See Booth, 2018). Many of these studies conclude that a changing climate is associated with spatial and temporal variation in exposure and transmission of each species of parasite. There are likely to be profound yet hard-to-discern changes to global patterns of parasitic disease transmission in the near, mid and long term (Slater and Michael, 2012). Some of these changes may be extreme enough to cause major shifts in distributions or even extinction of parasites, vectors and/or zoonotic hosts in localised, regional or even global contexts (Booth, 2018).

In forecasting these distributional changes, models have typically relied on parasites and their hosts’ responses to abiotic variables, while ignoring biotic interactions. A growing body of evidence emphasizes the importance of incorporating biotic interactions in developing accurate and precise distribution forecasts (Araújo and Guisan, 2006; Giannini *et al.*, 2013). Pickles *et al.*, (2013) is one of the few researchers to utilize SDM’s in modelling the impact of climate change on the whole host–parasite trophic cycle, while incorporating both abiotic and biotic interactions. They predicted an increase in habitat suitability for *Parelaphostrongylus tenuis* transmission across North America from now through to 2050 and 2080. By incorporating all components of the host–parasite trophic cycle allowed a refinement of forecasting parasite responses to climate change and provided a more conservative guide to shifting disease risk in the future.

However, Pickles *et al.*, (2013) focussed their research on one species of parasite, Carlson *et al.*, (2017) focussed on global parasitic species. Their goal was to project extinction risk of parasitic species using a patchwork of regionally and taxonomically specialized data sets which represent the best available distributional data sets in parasitology. This incredible data set captured the geographic ranges of 457 parasite species and their hosts. Their results suggest that 5 to 10% of these species are committed to extinction by 2070 from climate-driven habitat loss alone. By including biotic interactions, (host-driven coextinctions), models predict that up to 30% of parasitic worms are predicted to become extinct, driven by a combination of direct and indirect pressures. Carlson *et al.*, (2017) recommend expanding these analyses to the tremendous diversity of oceanic parasites (particularly for the speciose Cestoda, of elasmobranchs especially, and for unique specialists like Ozobranchus turtle leeches and cyamid whale lice that may be of special conservation interest) is a critical step forward (Carlson *et al.*, 2017).

## Marine SDM’s

Species Distribution Models have the majority of their grounding in the terrestrial realm, with their use in the marine realm growing over the last decade (Robinson *et al.*, 2011, 2017). Terrestrial SDMs are dominated by environmental variables, as these have shown to have an overriding control over the distribution of species. The marine realm poses a vast change from terrestrial realms as ecological factors such as dispersal, species interactions, and shifts in environmental requirements throughout life-history stages (i.e. ontogenetic shifts) are important in defining the distribution of species (Robinson *et al.*, 2011). These factors certainly play a role in land based models, but not to the degree that they might play in the three dimensional oceans.

The methods and examples mentioned above demonstrate that we truly are at a loss to accurately predict how biodiversity will be impacted by changing climate. Secondly, that the tools we have are incredibly powerful and are able to provide at least a partial insight into these cryptic communities. And finally, that biogeography is a multidisciplinary science with applications throughout biodiversity studies. There is a growing body of theoretical work and as these theories are being tinkered, toyed and experimented with, more and more information is being discovered. Biogeography is at the forefront of biodiversity studies, and by gaining insight into a unique and complicated lifestyle, this information could benefit our general understanding of how these ecosystems may fair in the coming storm.

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few studies have examined how changes in host specificity relate to spatiotemporal changes in environmental conditions [80,81]. Captur- ing the complex ways in which environmental filtering can affect realized host specificity is a looming challenge that calls for integrative approaches to consolidate the synergies between species distributions and biotic interactions [46]. For example, if variation in realized host specificity is linked to changes in regional host composition [40], a com- prehensive understanding of how environmental filters impact realized host specificity requires disentangling their effects on host species occurrence and on host–parasite interactions (i.e., by influencing epidemiological factors such as host susceptibility, parasite survival, and transmission potential). (wells and clark 2019)

## References