**Quantifying the contributions of dispersal and niches to diversity maintenance in a microbial system**

* Can we draw comparisons between island biogeography and astrobiology? Idea for an essay?

Aim of the investigation: to test the predictions of Chisholm *et al.,* 2016, by manipulating a microbial community in the lab

Robert H. MacArthur & Edward O. Wilson (1967) The Theory of Island Biogeography

* Seminal piece in island biogeography and ecology
* Popularized the theory that isolated communities maintain dynamic equilibrium between immigration and extinction rates
* Popularised the concepts and terminology of r/K selection theory
* Insular microcosms are common to all ecosystems, principles from island biogeography can be applied generally
* Postulates that insular species richness depends on island size and isolation from source regions.
* When there is an addition of the number of species on an island, the islands immigration rate of new species will decrease while the extinction rate of resident species will increase.
* There will be an equilibrial point where the immigration rate equals the extinction rate.
* Increase in island size will lower extinction curves while a decrease in distance between island and the source region will raise immigration curves.
* Intersection of these curves determines species number, they predict larger islands will have more species than smaller islands (assuming the islands are comparably isolated) and isolated islands will have fewer species than islands more proximal to source regions (assuming these islands are equally large).
* Additional discourse on how insular clusters and stepping stones affect this model.
* Survivorship theory – the probability for successful colonization is dependent on birth rate, death rate , and carrying capacity of the environment.
* Some species can be excluded from insular environments and the niche of a species can change after introduction.
* Pioneering species can be excluded because: the island has saturated levels of pre-existing competition, the pioneering species cannot maintain a population large enough to avoid extinction, and the island hosts too many or too few natural predators.
* When a species colonizes a new area, the species will either shift, expand or contract its realized niche.
* Three consecutive phases to the evolution of populations after colonization. Initially, there is a trend for colonizers to evolve from r-strategists (lots of offspring, little parental investment) into K-strategists (few offspring, increased parental investment).
* The founder effect (the loss of genetic variation that occurs when a new population is established by a very small number of individuals from a larger population) may also influence colonizing populations during this first phase.
* The second phase is marked by long term adaptations to the local environment. In this period, abilities for dispersal are commonly reduced, and colonizers will either differentiate or assimilate with competing species.
* In the third phase, the evolution of colonizing populations may result in speciation and/or adaptive radiation.
* Has been criticised for the interchangeability of species and islands, the independence between immigration and extinction, and the insignificance of non-equilibrial processes.

Stephen P. Hubbell (2001) The Unified Neutral Theory of Biodiversity and Biogeography

* MacArthur and Wilson’s work formed the bases of the unified neutral theory of biodiversity
* The hypothesis aims to explain the diversity and relative abundance of species in ecological communities, although like other neutral theory of ecology, Hubbell’s hypothesis assumes that the differences between member of an ecological community of trophically similar species are “neutral”, or irrelevant to their success.
* Implies that biodiversity arises at random, as each species follows a random walk (mathematical object, known as a stochastic or random process, that describes a path that consists of a succession of random steps on some mathematical space).
* Neutrality means that at a given trophic level in a food web, species are equivalent in birth rates, death rates, dispersal rates and speciation rates, when measured on a per-capita (individual) basis.
* This can be considered a null hypothesis or niche theory.

Harpole (2010) Neutral Theory of Species Diversity

<https://www.nature.com/scitable/knowledge/library/neutral-theory-of-species-diversity-13259703/>

Maintenance of biodiversity on islands (Chisholm *et al.,* 2016)

* MacArthur & Wilson (1967) proposed a general explanation for the maintenance of biodiversity on islands. Distance and area affect island species richness: large islands and islands nearer to maintains experience greater immigration than small, remote islands and should have more species at the colonization-extinction dynamic equilibrium.
* MacArthur & Wilson found empirical examples where this theory broke down. Archipelagos exhibit unusual species-area relationships (SARs): below a threshold island area, island species richness varies independent of area = the Small Island Effect.
* The small-island effect (SIE) violates M&A’s predictions AND it is an exception to the putative (general) ecological law that SARs should always be increasing functions – that the larger the area the more species you have.
* The prototypical (original/typical) example of SIE is for vascular plants in the Kapingamarangi Atoll in Micronesia but the phenomenon is general.
* Ecologists say – we need a general theory explaining the SIE whilst also incorporating class island biogeography results for large islands!
* Previous attempts to explain SIE have centred around two main hypotheses.
* 1) Extinction rates are independent of island area on small islands, because small islands are environmentally unstable and temporal turnover in species composition is rapid – species composition changes rapidly over time. Small islands are subject to major episodic disturbances that eliminate most life forms and thereby prevent species diversity from reach equilibrium.
* 2) Small islands have an unusual suite of habitats that is different from that on large islands. Certain types of habitat (e.g. riparian zones) are not available on small islands and this limits diversity.
* Shortcomings! They make no reference to immigration! They do not explain specifically how small islands could be exempt from the general island biogeographic rule that increasing island area means more immigration and more species (i.e. how the target area effect could disappear).
* The hypothesis that catastrophic disturbances induce the small-island effect is problematic because, even if disturbances do regularly wipe our species on small islands, the larger small islands should still receive more immigration and recover quicker than smaller small islands.
* The existing hypotheses appear to predict anomalously low diversity on small islands (relative to the SAW extrapolated from large islands), whereas the data show anomalously high diversity on small islands.
* Existing hypotheses are qualitative, without formulation in terms of quantitative models it is difficult to rigorously evaluate their success at explaining the small-island effect.
* Chisholm et al., postulate that diversity on both large and small islands is maintained by TWO mechanisms, niche constraints and immigration, but that niche diversity increases only slowly with area, whereas immigration increases rapidly with area.
* The net effect is that the niche constraints dominate on small islands (where immigration is low) but immigration dominates on large islands.
* 1) Test whether this combination of mechanisms can indeed produce biphasic island SARs by analysis a mechanistic mathematical model and fitting the model to 100 archipelago datasets.
* 2) Use the same datasets to test the theory’s key prediction that the transition between the two regimes of the SAR should occur at smaller island areas in archipelagoes where immigration is greater and for taxa that immigrate to islands more easily.
* MATHEMATICAL MODEL – Model includes immigration and niche structure, that allows one to specify how these vary with island area. Used previously published model that satisfies these conditions (Chisholm et al., 2010, 2011).
* Model is a simplified representation of island community dynamics, but adequate for testing the fundamental tenets of the theory in a general and parsimonious way.
* Model contains a local community (the focal island) and metacommunity (other islands and the mainland).
* Metacommunity comprises K equal-sized non-overlapping niches, and within each niche the species competing for resources are considered to be ecologically equivalent – the way they interact with the environment is the same. This means that the community dynamics within each niche follow neutral, zero-sum dynamics. At each time step, an individual is chosen at random to die in the metacommunity and is replaced by the offspring of another randomly chosen individual within the same niche.
* Speciation occurs in each time step with some typically very small probability. These processes lead to a speciation-extinction balance in the metacommunity and a species abundance distribution in each niche approximately equal to a log-series with parameters θ/K, where θ is known as Fisher’s α or the fundamental biodiversity number. Neutral theory predicts the existence of a fundamental biodiversity constant, conventionally written θ, that appears to govern species richness on a wide variety of spatial and temporal scales. Metacommunity diversity is considered to be fixed on time scale relevant to the island community.
* The island community in the model obeys similar dynamics to the metacommunity except that diversity is maintained only by immigration from the metacommunity (there is no speciation on the island). The island community comprises J individual organisms in K distinct equal-sized non-overlapping niches (as in the metacommunity, so that there are J/K = J\* individuals in each niche. At each time step, an individual is chosen at random to die in the island community and is replaced by the offspring of another randomly chosen individual within the same niche in the island community with probability 1 – m, or by a randomly selected immigrant from the same niche in the metacommunity with probability m. The probability m is typically small (i.e. immigrants are few and most propagules are produced locally on the island).
* DATASETS – Compiled 100 datasets of SARs for a range of taxa from a range of archipelago types, based on the synthesis of Lomolino & Weiser (2001). Only archipelagos with 10 + islands were included. Each archipelago was classified as terrestrial, montane, inland waters, or marine. The taxonomic group for each dataset was classified as birds, herpetofauna, invertebrates, mammals or plants.
* For each dataset, the number of individuals per unit area was taken from the original study or from other studies specific to the system where possible. In most cases, system-specific density estimates were unavailable and instead default values of densities for the taxa concerned were used, based on a literature survey.
* MODEL FITTING – For each archipelago dataset equation 2.5 was fit to the SAR data by finding the best-fit values of model’s three free parameters: the niche diversity K, the fundamental biodiversity number θ and the immigration parameter m.
* TESTING ACCURACY OF APPROXIMATE SPECIES-AREA RELATIONSHIP FORMULA – Compared exact species-area equation with the approximate species-area equation to assess the error in the latter. Achieved this by taking the best-fit parameter values for each dataset and evaluating both the exact and approximate formulae for those islands with estimated community size J = pA< 10 000.
* ESTIMATING CRITICAL AREA – For each archipelago dataset, they estimated the critical area Acrit at which the transition from the niche-structured to the colonization-extinction regime occurs by evaluating equation 2.8 for the fitted values of K, θ and m. This is a rigorous and repeatable method of estimating the critical area, but similar results could be obtained by other methods e.g. Lomolino (2001).
* The estimated critical area values were used to test the theory’s key predictions that the critical area should be larger in archipelagos that are more isolated and for taxa that are more dispersal limited.
* The project ran a multiple regression with log(Acrit) as the dependent variable, and archipelago type and taxonomic group as categorical explanatory variables. It is important to note here that there is no circulatory here because the information on the archipelago type and taxonomic group was used neither to fit the model nor estimate Acrit. The test is thus a strong test of our theory’s predictive capabilities.
* DISCUSSION – The proposed unified theory of island diversity can explain both the classic MacArthur & Wilson result of increasing diversity with island area among large islands, and the small-island effect of roughly constant diversity among small islands. According to this theory, the regime at small areas arises from niche constraints an the regime at large areas arises from a colonization-extinction balance. A mechanistic model of the relevant processes accurately fits 100 SARs from a broad range of archipelago types and for a braod range of taxa.
* The model used to test this theory is, to the best of their knowledge, the first mechanistic model fitted to datasets exhibiting the small-island effect. Past fits to similar data have been based on phenomenological models and the quality of the fits has been poorer.
* For example, Lomolin & Weiser (2001) fit piecewise linear models to almost the same data and achieved a mean R^2 of 0.69, compared with a mean R^2 of 0.91 for this model with the same number of free parameters. Though this model ignores much biological detail, it verifies the main hypothesis that a biphasic archipelago SAR can arise if niche diversity increases only slowly (or not at all) with area but the total number of immigrants increases rapidly with area.
* This theory also makes the prediction that the critical area (where the transition between the niche-structures regime and the colonization-extinction regime occurs) should be smaller where immigration is stronger. For example, it is usually easier for birds and plants to immigrate to islands than it is for mammals, and therefore our theory predicts Acrit to be smaller on average for birds and plants. Similarly, it is usually easier for organisms to immigrate to islands in inland waters than to oceanic islands, and so our theory predicts Acrit to be smaller on average for islands in inland waters. These predictions are largely borne out by the data.
* Overall the model accounts for roughly half the variance in the critical area (on a log scale) observed in island SARs, given only coarse information about taxonomic group and archipelago type. Previous explanations for the small-island effect cannot account for these patterns.
* This new theory encompasses two contrasting bodies of ecological theory: the niche structured regime corresponds to classic deterministic niche theories; the colonization-extinction regime corresponds to stochastic community theories such as the theory of island biogeography and neutral theory.
* In the niche structured regime, the identity of an island’s component species may change over time, but the total species richness is roughly equal to the niche diversity and could in principle be predicted by studying the abiotic properties of the system. As an example, consider a simplified caricature of an oceanic island, where one posits the presence of a tree niche, a grass niche, a salt-tolerant shrub niche, and so on, up to K niches. Then, under low immigration, our theory (in common with deterministic niche theories that suggest, in community ecology local, niche-based processes, such as environmental filtering, biotic interactions and interspecific trade-offs largely determine patterns of species diversity and composition) predicts the long-term coexistence of K species. The identities of these species may change over time, as very occasional colonization and extinction events occur within each niche, but the total number of species remains roughly equal to K.
* By contrast, in the colonization-extinction regime, the species richness is not predictable from the abiotic niche structure of the environment (which reflects climate, disturbance regimes, nutrient levels, geology) instead, average species richness could be predicted, in principle, from stochastic dynamic models parametrized with measured immigration and extinction rates.

Lomolino (1990) The Target Area Hypothesis: The Influence of Island Area on Immigration Rates of Non-Volant Mammals

* The larger the target area the higher the immigration rate. Winter immigrations by the canids (dog-like mammals), non-canids and all mammals combined increased significantly with island area. Thus, community structure of insular mammals in this and similar archipelagoes may be influenced by geometry of the islands and potential sources as well as the characteristics of the species and barrier in question.

Lomolino & Weiser (2001) Towards a more general species-area relationship: diversity on all islands, great and small

* Presents a general model of the species-area relationship that builds on traditional models, but includes the provision that richness may vary independent of island area on relatively small islands.
* Analysed species-area patterns for a broad diversity of insular biotas from aquatic to terrestrial archipelagos.
* Used breakpoint or piecewise regression methods by adding an additional term (the breakpoint transformation) to traditional species-area models. The resultant, more general, species-area model has three readily interpretable, biologically relevant parameters: the upper limits of the small island effect (SIE), an estimate of richness for relatively small islands, the slope of the species-area relationship (in semi-log, or log-log space) for relatively large islands.
* The SIE appeared to be a relatively common feature of the data sets studied. The upper limit of the SIE tended to be highest for species groups with relatively high resource requirements and low dispersal abilities, and for biotas of more isolated archipelagos.

Chisholm & Pacala (2010) Niche and neutral models predict asymptotically equivalent species abundance distributions in high-diversity ecological communities

* Fundamental challenge in ecology is to understand mechanisms that govern patterns of relative species abundance.
* Previous numerical simulations have suggested that complex niche-structured models produce species abundance distributions (SADs) that are qualitatively similar to those of very simple neutral models that ignore differences between species.
* In the absence of an analytical treatment of niche models, one cannot tell whether the two classes of model produce the same patterns via similar or different mechanisms.

Chisholm & Pacala (2011) Theory predicts a rapid transition from niche-structured to neutral biodiversity patterns across a speciation-rate gradient

* A central challenge in community ecology is to predict patterns of biodiversity with mechanistic models. Parameters in mechanistic model all have biological definitions. Conversely, phenomenological models seek to describe the data without worrying about what’s going on beneath the surface.
* The neutral model of biodiversity is a simple model that appears to provide parsimonious (frugal) and accurate predictions of biodiversity patterns in some ecosystems, even though it ignores processes such as species interactions and niche structure.

What conditions do I need to simulate with my experiment?

* I need to replicate archipelagos with different numbers of islands and different distances from each other and the mainland. Also, different types of archipelagos?
* Essentially need to replicate different island sizes and document species richness at these sizes. How are microbial communities affected by niche availability?
* Acrit (the point at which immigration takes over from niche availability as being the main mechanisms for diversity maintenance) should occur at a smaller island area for less isolated islands (those closer to the mainland).
* My experiment should emulate different island areas with varying distances from the mainland/other islands.
* We want to manipulate island area and immigration rate.

What do we know about island biogeography and microorganisms?

Locey (2010) Synthesizing traditional biogeography with microbial ecology: the importance of dormancy

* Dispersal limitation affects a species geographical range (Lomolino et al., 2006) and this affects speciation and extinction.
* A predominant hypothesis in microbial biogeography is that dispersal limitation is unimportant. The Baas-Becking hypothesis states that ‘everything is everywhere, but the environment selects’ (Baas-Becking, 1934) asserting that free-living microorganisms with highly resilient life stages can overcome dispersal limitation (de Wit & Bouvier, 2006).

What similar lab-based investigations have been done on microbial communities?

Dispersal Modifies the Diversity and Composition of Active Bacterial Communities in Response to a Salinity Disturbance

* For microorgamisms, the degree to which dispersal contributes to changes in community properties depends on 1) the magnitude of the dispersal rates, 2) the initial diversity of the communities undergoing dispersal, 3) the source of the immigrants.
* Water collected from two regions (marine and brackish) of the St. Lawrence Estuary using a Rosette sampler. Water from these sights served as both the medium and the inoculum.
* 200 L of the sampled water from each site was filtered through a 200 μm (micro meter) mesh into 30 L carboys to remove large zooplankton. The medium was subsequently filtered through 142 mm GF/F filters to remove protists.
* The microbial inoculum was prepared by further filtering the <200 μm water through a 25 μm mesh to remove large phytoplankton.
* The inoculum and medium originating from the marine site were stored in a constant temperature room at 4°C in the dark for 4 days until initiation of the experiment.
* The inoculum and medium from the brackish site were collected at the day when the experiment was started (August 30) and stored in the constant temperature room where the experiment was later performed.
* Dialysis tubing with a molecular weight cut-off of 12-14 kDA (kilodalton) was used to inoculate the microbial communities, as it ensured the free exchange of dissolved organic matter and nutrients without allowing the movement of microorganisms (protists, bacteria, viruses).
* Our choice of dialysis bags allowed the majority of organism molecules to diffuse efficiently, as the molecular mass of DOM (dissolved organic matter) in aquatic environments is typically smaller than 5kDA.
* Dialysis tubing pieces (45cm long) were rinsed thoroig

Lindstrom & Ostman (2011) The importance of Dispersal for Bacterial Community Composition and Functioning

Severin et al., (2013) Variable effect of dispersal on productivity of bacterial communities due to changes in function trait composition