**Chapter 1: What makes a great speciator?**

Diversification rates are known to vary across the tree of life (Grant and Grant 2002; Meyer 1993; Lovette 1993). Lineages that have diversified rapidly offer us the opportunity to study the drivers that influence the generation of biodiversity.

Oceanic archipelagoes have been considered natural laboratories for studying evolutionary processes because they play a key role in diversification (Coyne 2004; Whittaker 1998; Grant 1998; Price 2008). Geographically isolated populations often diverge making archipelagoes perfect scenarios for the rapid accumulation of species (Filardi and Moyle 2005; Mayr 1942). However, archipelagoes do not only accommodate high-diversifying lineages, but instead we find all the range from island birds that show little differentiation to very diverse lineages (Mayr and Diamond 2001).

Speciation on islands probably undergo different stages based on range expansions and contractions (Wilson 1961). In the first stages, young and good dispersive species restrict their distribution to the lowlands (Stages I: no differentiation (‘supertramp’) and Stage II: very differentiated (‘great speciator’)). Stages III and IV refer to the distribution of older and well-differentiated species that move upwards and colonise the higher regions of larger, often mountainous islands (Ricklefs & Bermingham 2002; Pepke et al. 2019; Gabrielli et al. 2020).

Mayr and Diamond (2001) introduced the concept of “great speciator” which has been repeatedly used despite being subjective and arbitrary. Great speciators show a high degree of interisland geographic variation, defined by their number of subspecies and allospecies. It has been proposed that great speciators may be either abundant, lowland species of intermediate dispersal ability and as good short-distance colonisers (Stage II; Diamond et al. 1976), or very good colonisers that suffer strong selection against dispersal ability after colonisation leading to sedentariness in a matter of generations (Diamond et al. 1976; Moyle et al. 2009).

I aim to revisit the great speciator concept by collating information on all bird lineages expanding Mayr and Diamond’s (2001) original sampling which only comprised birds from northern Melanesia (31 groups of birds were classified as great speciators (Mayr and Diamond 2001)). Among the potential questions to answer we can address:

1. **Do great speciators show high diversification rates? What are the main drivers?**

Great speciators are likely groups of birds that have radiated recently and rapidly, and are not necessarily sister taxa. It has been suggested geography plays an important role, but we also know that its importance has a limit because sharing the same distribution, some birds show many different morphs and some others do not diversify at all. Great speciators probably originate in a geographical region full of archipelagos where they have the opportunity to differentiate in a relatively short amount of time, but they are also likely to have a very specific set of life-history traits (short generation time, high clutch size and a generalist way of life) that make them so special.

1. **Are great speciators clustered in a specific geographical region? Are they restricted to Australasia and the Malay Archipelago?**

Great speciators probably suffer low seasonality so they can breed throughout the year and more than once, restricting their distribution to the tropics. Australasia and the Malay Archipelago provide the perfect scenario for birds to diverge: they are located close to the equator and there are many islands or different sizes close enough for birds to colonise.

1. **Dispersal and great speciators: Are great speciators also great dispersers?**

A reduction in dispersal ability following island colonisation has been invoked to solve “the paradox of the great speciators”. I expect to see two strategies: (i) some group of birds might show a range of dispersal abilities, with one or a few populations displaying high levels of dispersal and other (older) populations being sedentary, and (ii) other great speciators might show intermediate levels of dispersal ability. In the latter case, we should explore whether older lineages inhabit higher altitudes on larger islands (example of intra-island diversification e.g. *Zosterops borbonicus*) or they mainly inhabit lowlands.

1. **Do great speciators contain more species complexes than non-great speciators?**

I expect to see a positive relation between number of subspecies, diversification rate and number of species complexes within a genus.

1. **Are great speciators the product of one species with multiple subspecies or many species with a few subspecies each?**

This a more taxonomic question but as far as I have seen in the data great speciators seem to follow the second classification: they contain many species with a few subspecies each (e.g. *Zosterops* never has more than 17 subspecies). I do not know if this has biological relevance but I think it does not hurt to look at it.

**Methods**

I will collect data on the number of species and subspecies, range and presence on island from Avibase (<https://avibase.bsc-eoc.org/>), which incorporates taxonomic data from the major taxonomic publishers (Clement’s checklist, HBW/Birdlife, IOC checklist and Howard and Moore).

I have collected data on the number of species and subspecies from The Clements Checklist of Birds of the World (Cornell Lab of Ornithology) and I merged this dataset with the Hand-Wing Index (HWI) dataset from Sheard et al (2020) where data about body mass, range size, island presence, migratory status, habitat, territoriality, diet, latitude and annual precipitation are also available for 10339 species of birds. Subspecies-level information is not available but I will create a subset of potential great speciators based on their diversification rate**\*** (DR) and number of subspecies in the genus. Once I have a subset I will explore the number of islands where each subspecies is present and number of subspecies per island (if one or many). I will also collect morphological (e.g., weight, wing, bill or tarsus length), reproductive (e.g., age at first breeding, clutch size, egg mass, incubation period or type of young), and behavioural traits (type of nest, mating system or type of parental care). For those that live on islands I will collect also data of at which altitude they live to test the hypothesis that intra-island diversification can also be a strong driver of diversification (Wilson 1969).

**\*** Not publicly available yet but I’m in contact with Walter Jetz and he will get back to me once this dataset is uploaded to Dryad. Hopefully he won’t forget but I can always send him a nudge message or calculate DR myself.

**Preliminary results and data exploration**

To explore the data I created a subset based on number of subspecies per genus (>20 subspecies). This subset contained 77 genera, 740 species and 3698 subspecies in total.

As you can see in the attached figures all species classified as great speciators appear in the top 77 genera with greater number of subspecies. Interestingly, most of the genera in this subset come from Australasia and the Malay archipelago, although some spread through Africa or Eurasia and the number of subspecies living in Oceania is lower, but overall birds with high number of subspecies live in this region.

In the plot where you see island index\* plotted against number of subspecies you see that at the genera that have more subspecies and also a high island index are all within Mayr and Diamond’s great speciators. *Zosterops* seems to be the “greatest” speciator, with a very high number of subspecies but also a high island index.

\*Island Index = Association with islands: quantified as proportion of breeding/resident range intersecting with islands of landmass below 2,000 sq km (see Pigot et al. 2018 for more information)

\*\*The only great speciator that doesn’t appear in the plots is *Monarcha* which has suffered some changes to the genus *Symposiachrus.* I need to take a closer look at the current systematics.