SYNTHESIS

A short recap

I have shown that over evolutionary time, lineages expand and contract their ranges or disperse from one area to another and this leaves a trace in phylogenies. I have demonstrated that phylogenetic reconstructions are useful to detect the extent of species saturation at local scales and that regional limits to diversity are defined by range expansion which depends on geographic and ecological constraints (Chapter 1). The likelihood method I presented in Chapter 2 finds support for depth-dependent speciation in cichlids (Chapter 3); for songbirds, speciation rates are independent from elevational distribution (Chapter 4). For both cichlid fish and songbirds I find that rates of lineage movements across lake depths or elevations are not uniform (Chapters 3 and 4).

Did I analyze relevant traits for species selection? Did I analyze species selection at all?

Chapters 1, 3 and 4 showed that differences in chances of speciation is not always a consequence of dissimilarity in intrinsic traits but can also result from differences in geographic distribution. In Chapter 1, the per-lineage diversification rate depended on the geographic range size, a property that emerges at the species level, i.e. one of the characteristics of species selection according to Vrba (1984; see Introduction). In this same chapter, I showed that some species diversified more because they arose early in history and had enough time to expand and attain a large range which increased the resistance to extinction and foster speciation. The second characteristic of Vrba’s definition of species selection, heritability, was not met in Chapter 1 as the geographic range size of species was never inherited during speciation events (i.e., all species started out with range size = 1). Moreover, the neutral nature of the model used in Chapter 1 makes species similar in range size (hence in diversification rates) regardless of their phylogenetic relatedness as long as they are born around the same evolutionary time.

In the cichlid chapter (Chapter 3), I modelled the change from one depth range to another and found that shifts in diversification rate are associated to water depth (i.e., species experience different speciation regimes across depths). I also showed that daughter species inherit the same depth range as the parent species and I argued that depth-divergence plays a minor role in speciation. Therefore, by looking at the distribution of cichlids along the water column, I ultimately analyzed the evolution of a suite of traits that allow species to handle biotic and abiotic variables at a given depth. The same holds true for the analysis of diversification rates and elevation in songbirds (Chapter 4).

Ecological and evolutionary drivers could pull towards different directions
In Chapter 1, I documented that under certain circumstances, a clade with high rates of colonization yields a decrease in regional richness. One can imagine that if dispersal capacities are under selection and individuals with a highly-dispersive phenotype increase in frequency, richness would ultimately be affected. Examples where certain characteristics are selected but have negative consequences as side effect are scarce. An interesting example comes from Muir and Howard (1999) who showed that females of Japanese rice fish select larger males, although large-bodied males are associated with lower fecundity. In this case, sexual selection could drive the species to low levels of population size and increase vulnerability to extinction. Selection could in principle lead to extinction because the owner of a successful trait leaves more descendants than the other individuals, but the bulk of individuals that are far from the optimal trait value will eventually die and therefore the population decreases (Rankin and Lopez-Sepulcre 2005). Additionally, some frequency-dependent mechanisms can operate on successful individuals (Parvinen 2005). Perhaps these scenarios are likely to occur only in the presence of sudden environmental changes, which can accelerate selection and/or push species into the extremes of their fundamental niche space where they can survive but cannot reproduce (failure to reproduce; Congreve et al. 2018; Bisschop et al. 2019).

At the species level, a trait under selection can have positive effects in both the short term and the long term which leads to the intuitive prediction of a higher frequency of such trait. For instance, Vienne et al. (2013) developed theory to find that the maintenance of sexual reproduction (as opposed to asexuality) can be explained even if short-term advantages are not assumed but its prevalence is higher when sexual species have an ecological advantage (i.e., broader ecological niches).

Whether the outcomes of a trait under selection at the species level are different in the short or long term is almost unexplored (for an example in organisinal selection see Pruitt 2013). Recently, Blanchard and Moreau (2016) studied a tradeoff in defense syndromes in ants and documented that the presence of a sting is associated with decreasing rates of diversification while colony size or eye size (two other traits associated with defense) are linked to higher rates of speciation. They conclude that "selection to evolve a sting may be beneficial in the short term but ultimately suppresses rates of diversification over evolutionary time, as having a sting constrains a given clade from evolving other traits that are drivers of diversification". There is, however, no evidence to believe that ants tend to develop stings despite the lower rate of diversification associated with it. Van Valkenburgh et al. (2004) use teeth and jaw structure to determine the extent of dietary specialization and size evolution in canids (from the fossil record). They found that body mass increased substantially over time and transitions towards smaller sizes were minimal in such a way that small-bodied species disappeared. As mean body size increased, species evolved into specialized carnivores. They claim that, at the same time, highly-specialized species have short species longevity. However, what short-term processes cause evolution towards larger sizes is not clear. Furthermore, Van Valkenburgh et al. showed how transitions to large bodies are common even though this body size class often has a higher extinction rate.

A case study: species selection on body size in hummingbirds?

The body mass of animals has long been recognized as an important descriptor of ecological position, for instance, the classic studies on body size ratio showed that there is a constant difference in size between members of the same guild regulated by competition. Body size in flying animals is also determined by aerodynamic constraints (i.e., metabolic rates, energetic cost of flying and flight performance) which strengthen the ecological relevance of this trait. In hummingbird species, body size plays an additional role as predictor of antagonistic intraspecific interactions (Martin and Ghalambor 2014) because hummingbirds are highly specialized nectarivores which tend to monopolize floral resources and fiercely defend them from intruders (other hummingbird species). In summary, an optimal body size will be the result of physiological/mechanical constraints and ecological/behavioral interactions.

Hummingbird species differ in body mass which can be a consequence of the abovementioned constraints and interactions. It is then expected to see differences in species performance across body size which can be evaluated through the relative abundance of species.

Bribiesca et al. 2019 did an extensive literature search and collected information about the relative abundance of hummingbird species in local assemblages as well as their body size (three categories: small, intermediate and large). Using a Phylogenetic Generalized Linear Model, they concluded that species of intermediate size were locally the most abundant (Bribiesca et al. 2019). This suggests that intermediate-bodied species perform better at short ecological scales which raises the question whether this category of size is favored on an evolutionary scale as well.

To this end, I followed a similar methodology as in Chapter 3 where I used SecSSE to fit models with contrasting hypotheses on A) dependence of speciation/extinction on body mass class, B) different assumptions on trait evolution (three models: Constrained 1 rates, Constrained 2 rates and Constrained with 4 rates; see methods on Chapter 3), and C) the extent of inheritance of body size (the four main modes of speciation i.e., modes of trait inheritance; see methods on Chapter 3).

I used the body size categories mentioned earlier and the phylogenetic tree proposed by McGuire et al. (2014) to run all the model combinations (36 in total) with three starting points to prevent finding only local optima. The comparison across models was done by penalizing the number of free parameters (AICweights). For the five best supported ones,
I further explored whether a better fit was possible by including trait-dependent extinction or differences in transition rates between examined and concealed traits.

Table 1. Comparison of models of body-size dependent diversification in hummingbirds based on AIC weights. Models differ in what state transitions are allowed, and whether state shifts occur during speciation. Only the 10 best models are shown. CR = Constant Rates; CTD = Concealed trait-dependent; ETD = Examined trait-dependent. See methods in Chapter 3 for a full description of model assumptions.

| Dependence | Trait evolution model | Speciation mode | Qexamined ≠ Qconcealed? | Likelihood K | AICw | q
<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>CTD</td>
<td>Constrained with 4 rates</td>
<td>Dual inheritance</td>
<td>No</td>
<td>-991.29</td>
<td>8</td>
<td>0.99</td>
</tr>
<tr>
<td>ETD</td>
<td>Constrained with 4 rates</td>
<td>Dual inheritance</td>
<td>No</td>
<td>-1000.68</td>
<td>8</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>CTD</td>
<td>Constrained 2 rates</td>
<td>Dual inheritance</td>
<td>No</td>
<td>-1003.37</td>
<td>6</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>CTD</td>
<td>Constrained 1 rates</td>
<td>Dual inheritance</td>
<td>No</td>
<td>-1004.78</td>
<td>5</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>ETD</td>
<td>Constrained with 4 rates</td>
<td>Dual inheritance</td>
<td>Yes</td>
<td>-1000.68</td>
<td>12</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>ETD</td>
<td>Constrained with 4 rates</td>
<td>Single inheritance</td>
<td>No</td>
<td>-1010.75</td>
<td>8</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>CR</td>
<td>Constrained with 4 rates</td>
<td>Dual inheritance</td>
<td>No</td>
<td>-1014.75</td>
<td>6</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>CTD</td>
<td>Constrained with 4 rates</td>
<td>Single inheritance</td>
<td>No</td>
<td>-1013.65</td>
<td>8</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>ETD</td>
<td>Constrained 1 rates</td>
<td>Dual inheritance</td>
<td>No</td>
<td>-1016.69</td>
<td>5</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>ETD</td>
<td>Constrained 2 rates</td>
<td>Dual inheritance</td>
<td>No</td>
<td>-1016.30</td>
<td>6</td>
<td>&lt; 0.001</td>
</tr>
</tbody>
</table>

According to the best supported model, there is variation in per-lineage diversification rates among hummingbird species, and this heterogeneity in diversification rate is due to differential speciation rather than differential extinction. The difference in rates of origination cannot be explained by differences in body mass which suggests that there must be additional driver(s) in hummingbird diversification. I found that body size is likely to be inherited from ancestors to descendants which is in line with the results from a traditional phylogenetic signal analysis (i.e., Blomberg’s K and Pagel’s statistics; Bribiesca et al. 2019) indicating that body size evolution occurs between speciation events rather than during species divergence.

With this modest exercise, I have shown that species with intermediate size are ecologically dominant in local communities, but this advantage in fitness is not enough to increase their speciation (or decrease their extinction) rate. This analysis on two scales leads to the conclusion that body size is an ecologically relevant trait that is not subject to species selection.

What patterns in empirical data suggest that species selection acts on a clade? Can complex trait evolution mask species selection?

A phylogenetic reconstruction showing species-rich and species-poor subclades often draws attention and encourages the study of differential diversification in species. The asymmetric distribution of species in a tree might be due to a release of ecological limits or the result of acquiring a key innovation (Etienne and Haegeman 2012; but see Rabosky 2017). In Chapter 11 I found that neutral processes can also produce asymmetric trees, so the shape of phylogenies might not be informative on strict species selection. A high frequency of a certain trait state suggests that there is differential speciation but as I have shown, this is not enough to prove trait-dependent diversification as an operating mechanism in an SSE model. I conducted some very preliminary analyses where I simulated datasets under trait-dependent diversification and chose parameters values to obtain a frequency of traits that was rather balanced (i.e., there was no highly frequent trait state; this is possible because transition rates can homogenize trait state frequencies). Then, I ran SecSSE inference to find that trait-dependent diversification was well supported (which is very promising, as the signal of the process was correctly detected). Taken together, one can say that a skewed trait frequency is not necessarily evidence of trait-dependent diversification and at the same time, trait-dependent diversification can occur even in the absence of a skewed trait frequency. Perhaps there are many clades whose evolutionary dynamics depend on the evolution of a trait but do not produce visible frequency differences and are therefore often overlooked.

In the SSE framework, trait evolution is modelled as the switch from one state to another which is accurate for some traits but it might be oversimplified for others: epistasis, polygenic effects, transcription and environment are all examples of factors that can alter the realized trait state. In order to investigate the effect of complex trait evolution on the performance of SSE models, a master student Annabel Belliard and I considered a trait state (i.e., macrostate) as the result of the interaction of its parts (i.e., micro-components). One can think of animal diet (carnivore or herbivore) as the macrostate (trait state in traditional SSE notation) which would ultimately be determined by the combination of the micro-components such as gut biota, jaw morphology and tooth structure. In this study, we allowed micro-components to evolve independently and the macrostate (e.g., diet) be the result of this. We simulated trait evolution having an influence on diversification rates (Examined-trait dependent model; ETD) to produce phylogenetic trees with associated macrostate information. For the simulations, we used different combinations of transition rates q across micro-components and varied the number of micro-components. The relationship between micro-components and macrostates was given by three different sets of rules:

1) The additive model is a reflection of the threshold model of quantitative genetics, in which discrete traits originate from a polygenic mechanism. The organism expresses one trait state or another depending on whether the additive genetic effects surpass or stay below a certain threshold. In practice, a macrostate like carnivorous diet will be attained when the combination of micro-components favors this life style (e.g., two out of three micro-components are associated to carnivore: jaw and tooth morphology).
2) Two-level additive model: The two-level additive model is similar to the additive model, except that an intermediate level of micro-components, denoted meso-components, is present. The combination of micro-states would amount to a certain meso-component and the combination of them, determines the macrostate.

3) Full epistatic model: As the name suggests, the epistatic model is a simple representation of epistasis. Epistasis is a broad term defined as the interaction of two or more genes in a non-additive manner that yields a final phenotype. In contrast to the two previous models, all the possible combinations of micro-components are randomly assigned to a macrostate a priori (i.e., at the start of each simulation) and is used throughout the whole simulation. After each transition event, the sequence of micro-component states is re-evaluated and matched to its corresponding macrostate. Thus, the final macrostate does not depend on the prevalence of one microstate or the other, but rather on the specific sequence of micro-components, or more precisely, on their explicit role in contributing to the phenotype.

Finally, using SecSSE, we fit ETD, CTD and CR models and compared their statistical support (AIC) to count the instances where ETD was correctly identified as the best performing model.

We found that the initial combination of micro-components affects the performance of model selection: when parental macrostates have some variation, SecSSE is more likely to pick the signal of trait-dependent diversification. In general, high transition rates reduce accuracy in model selection and this effect is more pronounced in the additive model. The two-level additive model increased the number of instances that SecSSE did not show strong support for ETD model. Interestingly, the complexity of epistatic model does not compromise model selection, in fact, results of the epistatic model are similar to the simplest case of trait evolution. Overall, the number of micro-components did not have a major influence on the performance of SecSSE. It is important to note that for the additive model (in combination with high transition rates), the increase in the number of micro-components results in model selection becoming more similar to the case where a trait state does not depend on the integration of parts. In other words, high complexity in the internal structure of a trait (i.e., many micro-states) is equivalent to the traditional way how trait evolution is modelled in the SSE framework. Hence, after all, SSE models work fine even with complex traits, if the effect of the individual parts is additive. I expect that trait evolution analyzed in Chapter 3 has similar behavior where “depth-specialization” accounts for many morphological and physiological adjustments that independently evolve.

In the light of the development of the latest methods, how alive do I think species selection is?

Not much on species selection has been published lately, at least not using this term. Studies on differential rates of diversification across lineages as a function of trait variation have become popular, so researches have come to accept the importance of species selection in evolutionary dynamics without explicitly stating it. The attractive features of SSE models were somehow discredited when the tendency of false positives was pointed out (Rabosky and Goldberg 2015). Later, a return of SSE methods came with the “hidden” framework proposed by Beaulieu and O’Meara (2016). SecSSE is part of this revival and offers promising applications.

In Chapter 2 I found that SecSSE does not detect differences in diversification across trait states unless there is a strong relationship between the trait and diversification. The absence of evidence for trait-dependent diversification, however, cannot be interpreted as absence of species selection: the driver of origination and extinction of lineages might be a set of factors under selection which are, as a group, heritable. I think that for future researches, a very careful inspection of the hypotheses on trait evolution should be made, particularly the selection of the trait. If a trait is ecologically/evolutionarily relevant, it is expected that selection pressures could act in very particular ways. For instance flower structure could follow contrasting ways to evolve: one floral trait (corolla length) follows the punctuated model whereas another trait (pollination mode) shows more gradual changes and all of this has evolutionary consequences (Ibañez et al. 2019). Thus drivers of diversification might be very specific. I am particularly not very concerned about the dichotomy of the aggregate versus emergent nature of the traits that are potentially subject to selection. The most important part is to find those traits that can account for the variation in diversification rates across a clade, which is a challenge itself. Because the potential to trigger species divergence could reside in intraspecific variation, morphological or genetic variability within species can be a potential candidate to drive diversification (but see Kisel et al. 2012). Traits related to an increase or decrease in variability might be worth exploring, because, after all, as Lloyd and Gould (1993) said: “Species selection on variability is probably a major force of macroevolution”. Research on species selection has never disappeared altogether, and in the way I see it, there are now exciting paths to explore such as the potential conflict of ecological and evolutionary fitnesses.

Decades of research on ecology and evolution have shown that there is no one-explanation-fits-all for biodiversity patterns and so has this thesis. This thesis demonstrates that the determinants of diversity can include ecological and geographic constraints, environment specialization and lineage dispersal which suggests that the study of nature calls for the simultaneous analysis of broad spatial and temporal scales. Moreover, deep knowledge on the life history of taxonomic groups is fundamental to formulate ecological and evolutionary hypotheses. Although this sounds challenging, we are now in a privileged time when massive datasets, theory and techniques are being
developed at high pace. It is now when the best of the abilities of both naturalists and theoreticians should come together to understand how and why the number of species waxes and wanes across Earth.

REFERENCES


Harmon L.J., Harrison S. 2015. Species diversity is dynamic and unbounded at local and continental scales. Am. Nat. 185:000–000.


