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Avian diversification across space

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Chapter VIII: Synthesis and future recommendations

In this thesis, I focus on the influence of the extrinsic factor space on the evolution of birds at different scales; in chapters two and three at the intraspecific level, in chapters four and five between species, and in the last chapters at the scale of clades: in the case of the Passeriformes the level of order. Here, I present my main findings in a synthetic framework and provide recommendations for future research.

Main findings

In **chapter II** of this dissertation, I investigate the phylogeography of a widespread North American corvid, the Gray Jay (*Perisoreus canadensis*). The Gray Jay is a particular case, because there is strong evidence that its entire current distribution, which is strongly tied to the presence of spruce (*Picea* spp.), disappeared under ice sheets during the Last Glacial Maximum (LGM). Both vicariance and dispersal must thus have influenced the phylogeographic structure of the populations of the species. I found that Gray Jays reveal the typical structure of a northern organism, with multiple southern refugial populations, where the species weathered the LGM storm. Unlike other boreal organisms, northern Gray Jay populations are unusually genetically rich; a product of their withdrawal to multiple small isolated, coastal Arctic refugia, probably in Alaska, Haida Gwaii, and Newfoundland. I describe that Gray Jays thus show the inverse pattern found in most other boreal and arctic organisms; northern richness and southern purity. The study emphasizes that much remains to be discovered about past spatial population patterns, even in presumed relatively well-known temperate and boreal organisms.

In **chapter III** of my dissertation, I investigate the influence of dispersal and gene flow on the formation of intraspecific diversification in the Black-headed Grosbeak (*Pheucticus melanocephalus*), a widespread passerine species that occurs in multiple habitats and has a continuous distribution across a large part of the North American continent, with some minimal morphological diversification at the western and southern edges of its range. The species is furthermore a partial migrant, contributing to possible gene flow patterns. I find population structure between Pacific, western interior, and Sierra Madre de Sur populations, not unlike many other North American birds. However, there are strong levels of current gene flow, mostly from the interior of the distribution to the flanks, erasing past population structure. Mitochondrial haplogroups occur sympatrically in several locations, indicating strong potential for introgression. Nuclear genes involved do not show any particular geographic structure, another testimony of the rampant levels of gene flow within the species.

Chapters IV and V of this work focus on a highly dispersive group of Neotropical open-country birds, the pipits (*Anthus*). I first shed light on the taxonomy of the group using sequence and vocal data. One taxon, *Anthus peruvianus*, is basal to most of the clade of Neotropical pipits, and not embedded within *A. lutescens*, as previously thought, based on morphological evidence.

Furthermore, the species *A. furcatus* is made up of two highly divergent lineages, one Andean (*brevirostris*) and one in the southern South American lowlands (n nominate). Both deserve recognition as full species. The taxonomic groundwork at the intra-specific level is required for the analysis of diversification, because through it, we know which subspecies-associated lineages are on their own evolutionary trajectory, and which are better lumped as one lineage. I assessed diversification through vicariance by firstly investigating if there are any speed-ups in diversification at particular points in time, and relate these points in time to major geological events that may influence the diversification of a group of organisms of open habitats. The two most likely events are the Miocene spread of grasslands across the South American continent and, as in other groups, the shuffling of landscapes during the Last Glacial Maximum. This shuffling may have affected the Neotropical lowlands according to Hafferian Amazonian refuge hypothesis, or congruent with other theories of LGM landscape change in South America. LGM changes are also strongly associated with the Andean uplift, and any signature of LGM changes in diversification speed may be associated with either or both. We find a possible uptick in diversification at the end of the Miocene, but statistical evidence for the uptick is limited. I find that the formation of isolated populations and subsequent diversification played an important role in the geographic spread of the group over the South American continent. Over short distances, gene flow is pervasive, and in continuous blocks of habitat, genetic structure is close to zero, even over large distances, revealing that while dispersal contributes to gene flow over short distances, dispersal also aids diversification over larger distances (intermediate dispersal model).

Chapter VI of my dissertation presents the development of a novel method to assess the diversification dependent upon multiple trait states, while simultaneously correcting for type I error, which trait-dependent diversification analyses have traditionally been plagued by. The new method (implemented in the R package ‘SecSSE, “several examined and concealed state-dependent speciation and extinction”) is similar to the MuSSE approach by Fitzjohn et al. (2012), but incorporates a so-called concealed state (Beaulieu et al. 2016) to account for spurious positive relationships between the observed trait and diversification rates. The package also has other new functionalities not previously included in trait-dependent diversification analysis packages, such as the inclusion of an improved algorithm for conditioning on the survival of the root state, and the inclusion of an ambiguous state, in which a taxon can be assigned to multiple, or all, trait states. Using SecSSE, I test seven empirical data sets, ranging from a large amphibian phylogeny and associated data on warning coloration to leaf shape in epiphytic plants. All data sets have in common that they have been tested for trait-dependent effects of diversification using MuSSE. In five out of seven cases, inferences of trait-dependent diversification were premature and were actually better ascribed to a concealed trait. Simulations were used to test the reliability of SecSSE; while accounting for concealed-trait effects no significant statistical power is lost. The package was developed out of a need to analyze multistate elevation data in birds.

In Chapter VII I use the package ‘SecSSE’ to investigate the spatial diversification of passerines across an elevation gradient. In this chapter, I divide the elevational distribution of passerines into

different height categories and assess speciation, extinction, and dispersal (through transitions) across the different elevational zones. I find that across the entire passerine phylogeny, as well as other phylogenies of bird clades distributed across multiple elevation zones (9-primaried oscines, Furnariidae, Trochilidae), there are no differences in speciation rates between elevation zones. After ruling out the possibility that extinction rates vary across elevations, I conclude that the high diversity of passerines at mid-elevations may be best explained by greater amount of time for speciation to have accumulated many lineages (with the assumption that mountain ranges are geologically relatively young). I do find consistent differences in dispersal between different elevation zones; dispersal is greatest uphill and downhill from mid-elevations, and between adjacent elevation zones (supporting a gradient model). Dispersal from the tops of mountains into the lowlands is particularly infrequent.

Spatial evolution: lack of idiosyncrasy

The findings in my dissertation add to a growing body of evidence that the influence of space (and time) on evolution cannot be generalized. Gray Jays part from the usual pattern of northern depauperate populations, and Black-headed Grosbeaks show common phylogeographic patterns found in a multitude of North American organisms but the process by which population structure is shaped is very particular to the species. In pipits, the expected signature of landscape development on the evolution of the group was not confidently inferred; rather, even in this small group, various patterns and processes shape diversification. One would also expect a trait such as elevation, which affects a number of ecological, physiological, and genetic processes, to influence diversification in passerines. We cannot reject the hypothesis that diversification occurs at similar speed across different elevations. A tight link between space and diversification is not always available, and when found, leads to surprising results. While some studies have started to hint in the direction of a lack of idiosyncrasy in the spatial diversification of organisms (e.g. Smith et al. 2014, Zink et al. 2000), we are just starting to understand that unambiguous influences of space on the diversification of organisms are hard to infer, and perhaps do not exist, especially at larger phylogenetic scales, because they are confounded by the organisms' intrinsic characteristics or by other unexplored factors. Overall, these findings lead us away from traditional dispersalist versus vicariant thinking, but have to necessarily incorporate both factors, as well as others, in order to explain patterns.

Future directions

Chapter II and III indicate that while basic phylogeographic structure congruent with known biogeographic barriers may be relatively well known across at least temperate taxa, the processes underlying phylogeographic structure (and even in some cases the patterns) differ considerably across taxa. In a way, these two studies are a call for more single-species phylogeographic studies, to understand not only phylogeographic patterns (especially in poorly-sampled tropical taxa) and processes. It is at this phylogenetic level that we may be able to infer the processes driving diversification across space and at least tentatively relate them to organism-inherent characteristics. Morphological variation within species may offer some guidelines as to investigate

which species; they are often, but not always, indicators of phylogeographic patterns. Especially in cases where morphological patterns may indicate phylogeographical patterns that deviate from the restriction of known biogeographic barriers, further research is warranted to verify what spatial drivers could have shaped diversification.

Chapters IV and V reveal furthermore that even in a group of ecologically highly specialized birds, finding any relationship between ecological specialization (in the form of preference for grasslands) and the evolution of landscapes is difficult. Even at phylogenetically modest scales, there may be no idiosyncratic patterns of diversification correlated with events in Earth's history. Some of this may be due to particular life history characteristics inherent to this group; pipits are excellent dispersers. It may thus be necessary to not only pick a larger focal group, but also a focal group that has no secondary confounding characteristics to pinpoint to any relationship between Earth's history and diversification. Alternatively, one could compare several groups of contrasting characteristics (e.g. taxa of different habitats) and investigate if divergences within them correlate closely with particular geological events that shaped habitat formation, much as Smith et al. (2014) did with different groups of taxa on opposing sides of putative vicariant barriers.

In **chapters VI and VII** I show that there is no tight correlation between the speed of diversification and elevational distribution. This may reflect that the trait chosen, elevation in this case, is truly not linked to diversification. In chapter VI I showed that the method has relatively high power, so the conclusion of no link between diversification and elevation is solid. However, several traits may interact to jointly influence diversification. Although SecSSE partially accounts for these types of interactions, a fruitful focus of study may be to develop an improved method that can determine interactions of traits shaping diversification, and that can establish the relative influence of each of the traits. Thus, while again an idiosyncratic effect of elevation on diversification may be expected, I did not find this to be true, but elevation may act together with unexamined traits to drive diversification. Additionally, in large phylogenies, more confounding factors may distort or obscure the link between diversification and traits. Only after accounting for all these factors, a signal of trait-dependence may arise. Thus, while large data sets offer the possibility of increased statistical power, they also compromise finding correlations if correlations are not strong across a large number of tips in the tree. Intermediate-sized phylogenies thus offer perhaps the best testing grounds for detecting trait-dependent diversification. Nonetheless, perhaps an analysis including a large number of tips, such as mine, may show that correlations between a single trait and diversification across a large number of taxa are rare to non-existent.

Finally, space and time often interact to shape the diversification of organisms, and another avenue of research is the incorporation of the factor time in trait-dependent diversification analyses. Technically, this is very easy because such time-dependence can be readily built into the equations underlying SecSSE. This would allow us to correct for particular environmental conditions only existing during particular periods in geological time, provided knowledge on the absence or presence of traits in deep history is available.