

Charles University

Faculty of Science

Department of Ecology

HABILITATION THESIS



**Ecological specializations in avian assemblages
with a special focus on environmental gradients in Africa**

David Hořák

Prague, May 2017

To Dita, Anna and Ema

Was ich besitze seh' ich wie im Weiten, Und was verschwand wird mir zu Wirklichkeiten.

[What I possess seems far away from me, And what is gone becomes reality.]

Johann Wolfgang von Goethe

Contents

1. Preface.....	7
2. Acknowledgements.....	9
3. Introduction.....	11
4. Chapter 1	27
Hořák, D. , Sedláček, O., Reif, J., Riegert, J., & Pešata, M. (2010). When savannah encroaches on the forest: thresholds in bird–habitat associations in the Bamenda Highlands, Cameroon. <i>African Journal of Ecology</i> , 48(3), 822-827.	
5. Chapter 2	35
Reif, J., Hořák, D. , Sedláček, O., Riegert, J., Pešata, M., Hrázský, Z., Janeček, Š. & Storch, D. (2006). Unusual abundance–range size relationship in an Afrotropical bird community: the effect of geographical isolation? <i>Journal of Biogeography</i> , 33(11), 1959-1968	
6. Chapter 3	47
Djomo, N. E., Sedláček, O., Bayly, N., Ferenc, M., Albrecht, T., Reif, J., Motombi, F. N. & Hořák, D. (2014). Comparison of avian assemblage structures in two upper montane forests of the Cameroon volcanic line: lessons for bird conservation. <i>Biodiversity and Conservation</i> , 23(6), 1469-1484.	
7. Chapter 4	65
Ferenc, M., Fjeldså, J., Sedláček, O., Motombi, F. N., Djomo, N. E., Mudrová, K., & Hořák, D. (2016). Abundance-area relationships in bird assemblages along an Afrotropical elevational gradient: space limitation in montane forest selects for higher population densities. <i>Oecologia</i> , 181(1), 225-233.	
8. Chapter 5	77
Djomo N. E., Sedláček, O., Doležal, J., Dančák, M., Altman, J., Svoboda, M., Majeský, L. & Hořák, D. (2015). Relationship between Survival Rate of Avian Artificial Nests and Forest Vegetation Structure along a Tropical Altitudinal Gradient on Mount Cameroon. <i>Biotropica</i> , 47(6), 758-764.	

9. **Chapter 6**.....87
Hořák, D., Sedláček, O., Tószögyová, A., Albrecht, T., Ferenc, M., Jelinek, V., & Storch, D. (2011). Geographic variation in avian clutch size and nest predation risk along a productivity gradient in South Africa. *Ostrich*, 82(3), 175-183.
10. **Chapter 7**.....99
Hořák, D., Tószögyová, A., & Storch, D. (2015). Relative food limitation drives geographical clutch size variation in South African passerines: a large-scale test of Ashmole's seasonality hypothesis. *Global Ecology and Biogeography*, 24(4), 437-447.
11. **Chapter 8**.....113
Kopsová-Storchová, L., Storch, D., Brotons, L. & **Hořák, D.** (2017). Geographical Variation in Reproductive Investment across Avian Assemblages in Europe: Effects of Environmental Drivers Differ Between Altricial and Precocial Species. *Journal of Avian Biology*, in press.
12. **Chapter 9**.....127
Reif, J. & **Hořák, D.**, Krištín, A., Kopsová, L., Devictor, V. (2016): Linking habitat specialization with species' traits in European birds. *Oikos*, 125: 405–413.

Preface

Before I will start with an objective science, I find very important to explain shortly my internal motivation for working in this field by inserting a personal, strictly non-objective, and in fact a psychological preface. I hope, it will be interesting to readers as it facilitates overall understanding of why I think “what is crucial in ecology” and therefore worth of my studies. In addition, I intend to provide here a picture of my scientific focus development.

Being born in the lowland between two ridges of the Carpathian Mountains, I always admired diversity. Diversity of landscapes, diversity of habitats and of course diversity life forms. Note that it seems to be nothing special as humans generally like natural variation but on average I explored it in more detail than my friends and it made me really happy to be physically a part of nature. Now, I am aware that this positive relationship developed on emotional grounds and scientific exploration started as a child curiosity and “a need for action”, which sticks to me till now. I transformed my childhood passion for nature to birdwatching at the age of 10, approximately. Decision to be an ornithologist appeared not surprisingly with an important amount of inspiration from my boyhood friends with whom I travelled a lot while discovering the natural complexity, especially that of wetlands, surrounding my home town. Birds are amazing creatures, which are easy to understand for humans due to day time activity and visual orientation and absolutely fulfilled my aesthetic needs. Thus, I stayed with wetland birds during my master thesis, which focused on reproductive strategies of ducks. Counting and measuring eggs of Common Pochards brought me to the life history theory. I began with a sort of naive testing of life history predictions on duck models, which unfortunately did not satisfy fully my desire for abstract and complex questions... and, to be honest, I also suffered from a lack of appropriate scientific skills. At that period, I for the first time touched the issue of popularity of birds. Although it is obviously an advantage, huge amount of information we have about European birds also forces researchers to go for specific details of organisms’ relatively known lives instead of really exploring the big enigmatic parts of nature and natural phenomena as was the frequently case in the early history of ecology. I am little bit old fashioned in personality and stepping on unexplored grounds forms important part of my motivation to do science. Therefore, I did not hesitate when I had an opportunity to visit Africa – a truly unknown continent even in our times. Still finishing my PhD on ducks, I invested a lot of my time and energy to building up an avian research in Cameroon, focused especially on amazing biological diversity of the Cameroon Mountains. You can imagine that I wanted to transplant my knowledge of science from Europe to Africa, and – as usually – it did not work. I am and most likely always will be just a visitor to the tropics for whom it is rather unfeasible to collect nest information in scientifically sufficient sample size (*cf.* the work of Thomas E. Martin, who is capable to go in this way and has my admiration) because the tropical forest is really different and heterogeneous, tropical time is limited and avian breeding densities are (most likely!) incomparably low that those in the Czech Republic. We studied avian communities at that time and it seemed to be a

feasible and fascinating way of science in the African highlands, although the bird songs are not really similar to those in temperate zone. I became absorbed in community ecology and I think, this was the break point in my career because I found my current scope. Since then, searching for ways interconnecting avian communities and functional differences among birds is “a red line” of my work.

At the moment, I believe that differences between (avian) species and individuals (i) to some extent reflect the environmental variation within their ranges and habitats; (ii) have something to do with community compositions and consequently species richness patterns. In other words, I endeavour to reveal the links between spatial distribution, functional traits of birds and quality of their habitats. I see a scientific potential in such efforts and hope that resulting outputs will contribute to protection of disappearing natural environments.

Velký Tisý, July 2016

Acknowledgements

I met a lot of people, who influenced my life and my scientific career. Some of them provided a strong influence even they just walk around me, others worked with me for years. I really like taking pieces of inspiration from all and, obviously, it is often difficult to remember, who gave me a particular one. As a student I absorbed a lot of enthusiasm of Petr Musil, analytical skills of Tomáš Albrecht and general knowledge of David Storch. Work I value the most I did together with Ondra Sedláček and Jirka Reif. At the very beginning of our “African mission” we were a triple fitting together in skills and views as a jigsaw. Some very influential thoughts I obtained during discussions with Robert Ricklefs, Jon Fjeldså, Vincent Devictor and Jonathan Kingdon, whose insight and intellectual approach motivated me a lot to work in biodiversity. Thanks to my colleagues for fruitful collaborations and all my students, who did a lot of work to support my ideas. I am obliged to Adam Petrusek and Richard Machan for motivation not only to submit!

Above all, I am grateful to my family for infinite support and giving me food for personal growth.

During final stages, this work was supported by Czech Science Foundation (projects number P505/11/1617 and GB14-36098G).

Introduction

Since Alexander von Humboldt¹ noted a broad scale patterns in species richness, spatial variation in biological diversity has attracted much scientific attention. During past 200 years scientists invested huge efforts to explain increasing number of species towards the Equator – the most pronounced geographical gradient². According to Rahbek & Graves³ over 100 hypotheses proposed so far can be, however, reduced to five general factors, which are not mutually exclusive. High tropical diversity is then attributed to (i) high energy availability, (ii) longer evolutionary time available, (iii) higher habitat heterogeneity, (iv) larger area available, and (v) geometric constrains. These factors affect number of species via evolutionary (speciation and extinction rates)⁴ and ecological processes (niche space available, ecological specialization)⁵, which are supported by climatic stability of tropical regions over short (seasonality, ecoclimatic stability)⁶ and long time periods (*paleo*-ecoclimatic stability)⁷. In spite of the monumental knowledge we have nowadays, ecologists are still not satisfied and go for more details in search for a general “theory like” explanation, which, if can be afforded at all, is hidden in an enormous complexity of nature. Therefore, studies of spatial patterns in number of species are still a central goal of contemporary ecology.

Large scale biogeographical descriptions of many, particularly vertebrate, taxa distributions provides almost comprehensive picture at least within the (considerable) limits imposed by our mapping potential of temporal variation in distribution of individuals in space. Moreover, species’ geographical ranges are recently being polished by species distribution modelling approaches⁸. Indeed, from many points of view the combination of species distributions and environmental variables is well explored and thus more and more researchers rely on incorporation of additional information into biodiversity analyses, such as local population densities⁹, functional aspects i.e. variation in ecological traits among species, and phylogenetic relationships¹⁰. It is believed that this could shed more light on structuring local assemblages¹¹ or explain the ecological factors linked to speciation events¹². Overall,

¹ von Humboldt, A. & Bonpland, A. (1807). *Essai sur la géographie des plantes accompagné d’un tableau physique des régions équinoxiales*. Paris: Shoell, reprinted by Arno Press, New York.

² Gaston, K.J. (2000). Global patterns in biodiversity. *Nature* 405: 220-227.

³ Rahbek, C., & Graves, G. R. (2001). Multiscale assessment of patterns of avian species richness. *Proceedings of the National Academy of Sciences*, 98(8), 4534-4539.

⁴ Weir, J. T., & Schluter, D. (2007). The latitudinal gradient in recent speciation and extinction rates of birds and mammals. *Science*, 315(5818), 1574-1576.

⁵ Connell, J., & Orias, E. (1964). The Ecological Regulation of Species Diversity. *The American Naturalist*, 98(903), 399-414.

⁶ Fjeldså, J., Lambin, E. and Mertens, B. (1999), Correlation between endemism and local ecoclimatic stability documented by comparing Andean bird distributions and remotely sensed land surface data. *Ecography*, 22: 63–78.

⁷ Fjeldså, J., & Lovett, J. C. (1997). Biodiversity and environmental stability. *Biodiversity & Conservation*, 6(3), 315-323.

⁸ Araújo, M. B. and Guisan, A. (2006), Five (or so) challenges for species distribution modelling. *Journal of Biogeography*, 33: 1677–1688.

⁹ Reeve, A. H., Borregaard, M. K. and Fjeldså, J. (2016), Negative range size–abundance relationships in Indo-Pacific bird communities. *Ecography*, 39: 990–997.

¹⁰ Monnet, A.-C., Jiguet, F., Meynard, C. N., Mouillot, D., Mouquet, N., Thuiller, W. and Devictor, V. (2014), Asynchrony of taxonomic, functional and phylogenetic diversity in birds. *Global Ecology and Biogeography*, 23: 780–788.

¹¹ Petchey, O. L., Evans, K. L., Fishburn, I. S., & Gaston, K. J. (2007). Low functional diversity and no redundancy in British avian assemblages. *Journal of Animal Ecology*, 76(5), 977-985.

I find it a promising step in understanding spatial biodiversity patterns in terms of species density and functional diversity. Indeed, species of rich tropical regions differ in several functional aspects from their temperate zone counterparts. This has been well described in birds, for which we have been able to collect huge amount of information during past decades. The first steps, however, date back to Humboldt, Darwin and Wallace, who brought up an exciting descriptive evidence of natural diversity and made efforts to explain it ecologically. Later Moreau, Lack and Skutch set foundations of modern life history theory in the first half of the 20th century while explaining clutch size variation in birds^{13,14,15}. Since then the environmental distinction between temperate and tropical regions is frequently utilized as an ecological background for explaining life history evolution.

In summary, we have quite precise information about how species (and consequently species richness) are distributed across the globe or generally in space. We already know that different geographical regions support functionally different species, although much information about functional variation is missing especially from tropical regions. On the top of that, we have the evidence that spatial change in functional aspects of life is correlated with environmental variation, even though important mechanistic details are still missing, and also with gradients of species richness. However, the mechanisms explicitly linking functional traits or way of life to the number of coexisting species are almost lacking. Do functional differences among (tropical) species directly link to high levels of species co-existence? Or are they determined independently by same or similar environmental factors? Are they even completely independent? Answers to these questions are difficult to find and they are really attractive from pure scientific as well as conservational point of view as they may elucidate how *quantity* and *quality* of nature are connected.

To find a mechanistic link between community structure and ecological specializations of its members seems to be a difficult task. It is a question of field data availability – such as details about ecological space use – and also a matter of concepts, which are frequently missing. The potential solution lays in reducing the issue into smaller components such as link between environment and traits or trait space structure (functional diversity) and species richness, and start with utilisation of rough e.g. *macroecological* data, which provides relatively complete set of species and reasonable variation in focal variables. I have been trying to do it, in other words to adopt *a functional perspective* on diversity patterns. What I see behind “*a functional perspective*”? Primarily, I understand *a function* in an Eltonian sense as *a role* of an organism in an ecosystem i.e. a quality of an organism¹⁶. It combines habitat and diet specializations, morphological adaptations, reproductive strategies etc. and

¹² Ricklefs, R. E. (2012). Species richness and morphological diversity of passerine birds. *Proceedings of the National Academy of Sciences*, 109(36), 14482-14487.

¹³ Moreau, R. E. 1944. Clutch size: A comparative study with reference to African birds. *Ibis* 86:286-347.

¹⁴ Lack, D. (1947). The significance of clutch-size. *Ibis*, 89(2), 302-352.

¹⁵ Skutch, A. F. 1949. Do tropical birds rear as many young as they can nourish? *Ibis* 91:430-455.

¹⁶ Devictor, V., Clavel, J., Julliard, R., Lavergne, S., Mouillot, D., Thuiller, W., ... & Mouquet, N. (2010). Defining and measuring ecological specialization. *Journal of Applied Ecology*, 47(1), 15-25.

it is believed that it can be, to some unknown extent, described by traits. *This role* is modified (selected) by the environment by so called habitat filtering¹⁷ and adjusted by the surrounding community e.g. by limiting similarity¹⁸, however other mechanisms are possible. Broadly, I am currently interested in how traits vary in space and how this variation can be attributed to environmental changes. And, from the other side, how species richness patterns in space are interweaved with ecological specializations at the community or individual species level. Besides, there is an important aspect of avian specializations – population density. Grinnell defined a niche as a species specific *habitat*¹⁹. The actual realized niche or the habitat suitability can be measured simply by abundance, specifically, by its change along an ecological gradient. Thus, local abundances or population densities are crucial aspect of avian specializations as I see it and, moreover, they can be viewed as a trait i.e. being species specific but still having an intra-specific variation.

Africa

During my early career, I was lucky to visit the tropical Africa and start an ecological research there. Africa is an amazing continent and it is vastly unexplored even in comparisons with other tropical regions. It is poorly known due to its relative isolation – Sahara desert made a barrier for animals and humans as well – and of course due to political instability. Therefore, ecological research in Africa is limited and our knowledge of African birds is relatively low if compared to neotropical region for instance. Anyway, to an ecologist, Africa offers a lot of interesting subjects of studies, diversified environments, still untouched places and, from my perspective above all, excellent ecological gradients. Gradients of elevation along slopes of the high mountains such as Mount Kilimanjaro or Mount Cameroon, together with aridity gradients from Sahara southwards or almost longitudinal one in Southern Africa are above the most important from a large scale perspective. Habitat degradation specifically deforestation unfortunately forms a small scale gradients within savanna-forest mosaic of great importance for nature conservation.

Diversity in the tropical mountains

When I first visited Africa in 2003, I spent two months of field work in the Cameroon Mountains settled above 2,000 meters of elevation. To be honest, this was partly a practical decision as the climatic conditions, natural world and even health risks are much similar to Europe there than in lowlands. However, I soon discovered the uniqueness of this place. Tropical mountains are extremely

¹⁷ Van der Valk, A. G. (1981). Succession in wetlands: a Gleasonian approach. *Ecology*, 62: 688-696.

¹⁸ MacArthur, R. & Levins, R. (1967). The limiting similarity, convergence, and divergence of coexisting species. *The American Naturalist*, 101:377-385.

¹⁹ Grinnell, J. (1917) The niche relationship of the California Thrasher. *The Auk*, 34, 427–433.

rich in diversity. From a larger perspective, they form a hot spot on global map of species richness²⁰. Besides, they host high numbers of endemic (restricted range) species, which are frequently endangered ones²¹. These facts make the tropical mountains an excellent laboratory for scientists asking for factors behind the mountain richness and also target location for nature conservation as destruction of such places leads undeniably to great biodiversity losses. Why mountains in tropics are so rich is currently one of the leading questions in ecology. It is usually attributed to (i) climatic stability²², (ii) environmental productivity²³ and (iii) huge topographic variation at landscape scale²⁴. The last point results in numerous ecological gradients at relatively small spatial scale and geographical isolation of mountains tops, which resembles oceanic islands²⁵. This in turn promotes spatial segregation and potentially high species turnover in space. *Therefore, if ecological specialization has something to do with species richness patterns, it happens on tropical mountains!*

Birds of the Bamenda Highlands

My African research started in the Bamenda Highlands in the north-western part of the Cameroon volcanic line in West-Central Africa, which is a truly unique place and extremely exciting destination for a biogeographer. The Cameroon volcanic line forms “a sky archipelago” of tectonic and volcanic origin isolated from other high mountains in the East Africa by thousands of kilometres. It has an unclear chronological history, however, the majority of the mountain range was uplifted during the Cenozoic, the Bamenda Highlands likely from the Oligocene to Miocene and the highest peak – Mount Cameroon – is still active²⁶. Species diversity and high rate of endemism are thought to be a result of speciation during the region's long and complex orogenic history^{27,28}. Especially the upper montane habitats host numerous restricted range species – 30 endemic bird species are found in the Cameroon Mountains²⁹. At the end of the 19th and beginning of the 20th century, the region has attracted a lot of scientific attention but rather of classical taxonomically oriented zoologists such as

²⁰ Davies, R. G., Orme, C. D. L., Storch, D., Olson, V. A., Thomas, G. H., Ross, S. G., ... & Blackburn, T. M. (2007). Topography, energy and the global distribution of bird species richness. *Proceedings of the Royal Society of London B: Biological Sciences*, 274(1614), 1189-1197.

²¹ Orme, C. D. L., Davies, R. G., Burgess, M., Eigenbrod, F., Pickup, N., Olson, V. A., ... & Stattersfield, A. J. (2005). Global hotspots of species richness are not congruent with endemism or threat. *Nature*, 436(7053), 1016-1019.

²² Fjeldså, J., Bowie, R. C., & Rahbek, C. (2012). The role of mountain ranges in the diversification of birds. *Annual Review of Ecology, Evolution, and Systematics*, 43, 249-265.

²³ Ruggiero, A., & Hawkins, B. A. (2008). Why do mountains support so many species of birds? *Ecography*, 31(3), 306-315.

²⁴ Rahbek, C., & Graves, G. R. (2000). Detection of macro-ecological patterns in South American hummingbirds is affected by spatial scale. *Proceedings of the Royal Society of London B: Biological Sciences*, 267(1459), 2259-2265.

²⁵ Mayr, E., & Diamond, J. M. (1976). Birds on islands in the sky: origin of the montane avifauna of Northern Melanesia. *Proceedings of the National Academy of Sciences*, 73(5), 1765-1769.

²⁶ Marzoli, A., Piccirillo, E. M., Renne, P. R., Bellieni, G., Iacumin, M., Nyobe, J. B., & Tongwa, A. T. (2000). The Cameroon Volcanic Line revisited: petrogenesis of continental basaltic magmas from lithospheric and asthenospheric mantle sources. *Journal of Petrology*, 41(1), 87-109.

²⁷ Louette, M. (1981). Birds of Cameroon: an annotated checklist. *Verhandlungen van de Koninklijke Academie voor Wetenschappen, Letter en Schone Kunsten van België*, 43, 1-295.

²⁸ Stuart, S. N. (Ed.) (1986). *Conservation of Cameroon Montane Forests*. Cambridge, UK: International Council for Bird Preservation.

²⁹ BirdLife International (2016) Endemic Bird Area factsheet: Cameroon mountains. Downloaded from <http://www.birdlife.org> on 19/08/2016

Reichenow, Bannerman and Serle^{30,31} than ecologists *sensu stricto*. Although some basic ecologically relevant data were collected during these ornithological surveys^{27,28}, interpretations of ecological patterns were rather scarce. I think, it was because the analytical ecology was a young discipline at that time. Thus, ecological questions vastly remain to be tested on avian systems of the region.

Most of the Cameroon Mountains' tops are covered or naturally would be covered by the montane forest – due to the location within a cloud zone³², it is a cold and humid forest type with a lot of epiphytes. It is assumed that its distribution underwent important changes during the Quaternary³³. It was distributed in lower altitudes in glacial periods where it probably merged with the lowland forest, forming an environment with a continent-wide distribution. Conversely, in periods of global climatic optima, the montane forest retreated to higher altitudes and became fragmented, such as recently when it has a lower elevation limit at altitudes of about 1600 m a.s.l.³⁴ in the Cameroon Mountains. I first worked in the mosaic landscapes of the mount Oku region. The former montane forest here was unfortunately replaced by pastures, fields and burned areas during past decades. This kind of human activities is widespread in the region and strongly influences the local natural environments. Still, in the upper parts of the mountains, forest patches survived in inaccessible places such along streams in the valleys and still host specialist bird species, which we found in relatively high abundances³⁵. Later, we conducted several field trips to the Kilum-Ijim forest, which is situated around the summit of Mount Oku. In fact, it is the largest remnant of the montane forest in West-Central Africa, although it covers only 20,000 ha³⁶ and it is surrounded by the savannah inhabited by dense human population. With a crater lake bellow the summit at 2,200 m asl, it was an extraordinary experience for a naturalist and besides it provided a valuable scientific data for comparison of avian communities between the true forest and the forest patches within the mosaic landscape. We found that some of the species are missing from the degraded forest patches or have low abundances, mostly those requiring medium to large home ranges such as *Apaloderma vittatum*. However, some of species tolerate the fragmentation to some extent. For instance, *Tauraco banermanni*, an endemic species to the Bamenda Highlands, survives quite well in the mosaic landscape most likely because it operates over very large spatial scale utilizing different fragments. This might be related to its body size in combination with

³⁰ Bannerman, D. A. (1915). Report on the Birds collected by the late Mr. Boyd Alexander (Rifle Brigade) during his last Expedition to Africa.-Part V. List of the Birds obtained in the Manenguba Mountains (Cameroon). *Ibis*, 57(4), 643-662.

³¹ Serle, W. (1954). A second contribution to the ornithology of the British Cameroons. *Ibis*, 96(1), 47-80.

³² Scatena, F. N., Bruinzeel, L. A., Bubb, P. & Das, S. Setting the stage (2010). *Tropical montane cloud forests* (ed. by L. A. Bruinzeel, F. N. Scatena & L. S. Hamilton), pp. 3-13. Cambridge University Press, UK.

³³ Elenga, H., Peyron, O., Bonnefille, R., Jolly, D., Cheddadi, R., Guiot, J., ... & Hamilton, A. C. (2000). Pollen-based biome reconstruction for southern Europe and Africa 18,000 yr bp. *Journal of Biogeography*, 27(3), 621-634.

³⁴ Thomas, D.W. (1986) Vegetation in the montane forests of Cameroon. Conservation of Cameroon montane forests (ed. by S.N. Stuart), pp. 20–27. International Council for Bird Preservation, Cambridge, UK.

³⁵ Reif, J., Hořák, D., Sedláček, O., Riegert, J., Pešata, M., Hrázský, Z., ... & Storch, D. (2006). Unusual abundance–range size relationship in an Afromontane bird community: the effect of geographical isolation? *Journal of Biogeography*, 33(11), 1959-1968.

³⁶ BirdLife International (2016) Important Bird and Biodiversity Area factsheet: Mount Oku. Downloaded from <http://www.birdlife.org> on 23/08/2016

prevailing frugivory³⁷. This is not bad news for this endangered species. Surprisingly, we found that *Laniarius atrofasciatus* – a charismatic “black & yellow” member of Malaconotidae family – seems to have similarly high population densities in the mosaic landscape and in the forest interior. Was this species specialized for open areas within the forest? Based on the data and field experience this does not seem to be the case. *Laniarius* lives in the forest undergrowth, thus it is only weakly affected by cutting the trees above. I speculate that it rather profits from more bushes or less intense inter-specific competition in the degraded environment. To sum up, we found that montane forests around Mount Oku, even those in patches, still host reasonable abundances of locally specialized species, although the effect of fragmentation likely depends on their ecological traits such as micro-habitat specialization, diet preference, or body mass.

When two environments come into contact as it is in the case of the savanna and the forest in the Bamenda Highlands, two avian communities necessarily meet and presumably interact by penetrating from one to another environment. This is an interesting local scale phenomenon as it tells us something about native habitat affinity of particular species/communities or even more interestingly about “habitat view from an avian perspective”. In the latter case, I expect that birds native to “A habitat” that occupy suitable patches in “B habitat” in fact distinguish the habitat more finely than it is defined, and/or require less area of respective habitat for survival – this might be influenced by definition, few trees vs. forest. I tested the thresholds in bird-habitat associations along forest-savanna gradient and found striking difference between the birds of savanna origin and those from the forest³⁸. Savanna species almost do not invade the forest, even not the forest gaps, although exceptions exist³⁹. They strictly view it as something different or maybe cannot win in competition with natives i.e. bear less suitable adaptations (?). On the other hand, the forest species can be found quite frequently in the small groups of trees or bushes within the open landscape. They are thus relatively tolerant to habitat fragmentation. Is it a question of space available, I mean do they require smaller area of suitable if compared to open land species, or see a group of trees as a forest? Both can hold. The tree cover is higher than grassland, thus the same surface area of the forest generally offers bigger volume of ecological space than similar area of grassland. In consequence, a small patch of the forest may offer enough resources for forest species. This requires a rigorous testing in the future.

In the Afromontane forests, we further tested one of the macroecological rules: abundance-range size relationship^{40,41}. This empirical rule described mostly from temperate zone regions states

³⁷ BirdLife International (2016) Species factsheet: *Tauraco bannermani*. Downloaded from <http://www.birdlife.org> on 23/08/2016.

³⁸ Hořák, D., Sedláček, O., Reif, J., Riegert, J., & Pešata, M. (2010). When savannah encroaches on the forest: thresholds in bird-habitat associations in the Bamenda Highlands, Cameroon. *African Journal of Ecology*, 48(3), 822-827.

³⁹ At mid-elevations of Mount Cameroon, forest elephants (*Loxodonta africana*) has cleared the forest creating vast areas of *Afromomum* plants and grasses. This open habitat closed by the forest is inhabited by *Cisticola chubbii* a non-forest specialist, which can survive here thanks to large scale of clearings.

⁴⁰ Brown JH (1984) On the relationship between abundance and distribution of species. *The American Naturalist* 124:255–279.

⁴¹ Gaston KJ, Blackburn TM, Greenwood JJD, Gregory RD, Quinn RM, Lawton JH (2000) Abundance-occupancy relationships. *Journal of Applied Ecology* 37:39–59.

that local abundances are positively correlated with species' geographical range size. This is in fact a correlation of abundances across scales, for which quite a lot of mechanisms have been suggested. In addition to methodological issues such as incomplete sampling^{42,43}, mechanistic explanations include (1) resource use and availability—species utilizing a wider range or more abundant resources becoming most abundant and widely distributed^{40,44}; (2) vital rates—high population growth rate leading to high abundance and more occupied sites⁴⁵; or (3) dispersal—intensive dispersal among sub-populations of individual species producing a positive inter-specific abundance-range size relationship⁴⁴, for review see Borregaard & Rahbek⁴⁶. In contrast to expectations we found in the mosaic landscape of the Bamenda Highlands, that there is no relationship between abundance and geographical distribution³⁵. Further analyses revealed that mostly high abundances of endemics and species strictly confined to montane forests, both of which occupy small ranges, disturb the pattern. From the conservationist point of view, this is a good message. Endangered species of birds from African mountains still hold high population densities and thus are a meaningful target of protection actions. One may argue that no action is needed if such birds are obviously fine even in degraded environments. However, such a conclusion is likely affected by the time lag between forest destruction and declines of populations. The deforestation started in the second half of the 20th century⁴⁷ and it is highly probable that populations of birds will decline more in the early future as a response to it. From a pure scientific view high abundances of endemics are attractive as well. Why restricted range species in tropical mountains hold high population densities? From mechanisms listed above, ecological specialization to local conditions is discussed most frequently in the context of birds and it is argued that long term climatic stability of the region enabled this²².

As our study³⁵ was among the first documenting this pattern from tropical mountains, I later decided to go deeper into understanding this pattern and continued with collection of the similar data on another mountain for comparison. Mount Cameroon is the highest peak of the Cameroon volcanic line and of the whole West-Central Africa. It reaches up to 4,095 m asl. This active volcano is located at the sea coast in the Gulf of Guinea and isolated from other mountains of the range. Thus, it has a very hot climate and receives locally huge amount of rainfall each year, ranking with its up to 12,000

⁴² Bock CE, Ricklefs RE (1983) Range size and local abundance of some North American songbirds—a positive correlation. *The American Naturalist*, 122:295–299.

⁴³ Komonen A, Paivinen J, Kotiaho JS (2009) Missing the rarest: is the positive interspecific abundance-distribution relationship a truly general macroecological pattern? *Biological Letters*, 5:492–494.

⁴⁴ Hanski I, Kouki J, Halkka A (1993) Three explanations of the positive relationship between distribution and abundance of species. In: Ricklefs RE, Schlüter I (eds) *Species diversity in ecological communities: historical and geographical perspectives*. University of Chicago Press, Chicago, pp 108–116.

⁴⁵ Holt RD, Lawton JH, Gaston KJ, Blackburn TM (1997) On the relationship between range size and local abundance: back to basics. *Oikos* 78:183–190.

⁴⁶ Borregaard MK & Rahbek C (2010) Causality of the relationship between geographic distribution and species abundance. *The Quarterly Review of Biology*, 85:3–25.

⁴⁷ Ndenecho, E. N. (2005). Savannization of tropical Montane cloud forests in the Bamenda Highlands, Cameroon. *Journal of the Cameroon Academy of Sciences*, 5(1), 3-10.

mm of annual⁴⁸ precipitation among the wettest places in the world. Recent volcanic activity presumably together with a human induced burning causes that the tree line is extremely low if compared with other tropical mountains. At about 2,300 m asl the tropical montane forest sharply changes in the montane grassland. However, the montane forest is extremely well preserved here and at its upper parts it is nicely comparable with more inland located, drier and colder Mount Oku, the second highest peak of Cameroon (3011 m asl). To compare the same montane environments on two different mountains, which are ~ 260 km apart, we employed the same point count approach to estimate community structures⁴⁹. In general, both communities were quite similar. Two species of birds are strictly endemic to Mount Cameroon – Mount Cameroon Francolin (*Francolinus camerounensis*) and Mount Cameroon Speirops (*Speirops melanocephalus*). Some species from Mount Oku do not occur on Mount Cameroon such as Orange tufted Sunbird (*Cynniris bouvieri*), which is however, rather an open landscape species. Avian community on Mount Oku is more species rich due to presence of more widespread species, which is likely a result of heterogonous landscape context of the mountain. Besides, humans frequently enter the forest interior on Mount Oku, which might influence the forest structure, although this is difficult to detect based on the forest morphology in the field. Still spatial turnover of avian species is higher there, suggesting higher heterogeneity of vegetation. Unfortunately, although collected, forest composition data remains to be analysed. For birds, most importantly we found that local abundances of restricted range species are high on both mountains (leading to distorted abundance-range size relationships) but if the same species were compared between the mountains, we found higher abundances on Mount Cameroon. Understanding this difference has a potential to shed some light on high abundances in the tropical mountains in general. I am convinced that the observed difference is real and can be attributed to (i) quality of the forests itself, or (ii) quality of the landscape context. Mount Cameroon montane forest is more pristine, surrounded by lowland forest i.e. by similar environment and definitely human activities are less important there. Besides, Mount Cameroon montane forest is obviously more productive due to warmer and wetter climate. Therefore, I offer two explanations. First, Mount Cameroon and its surroundings is less impacted by humans, which positively affects avian population densities. Second, Mount Cameroon higher productivity provides more food resources to birds, which can consequently afford higher population densities. Both scenarios are likely not mutually exclusive. Theoretically, they can be distinguished by investigating other mountains with different combination of environmental factors or future repeated surveys, say in 10 or 20 years, on the same mountains may suggest the importance of human impact – if the population densities on Mount Oku will be even lower, then the probability of the role of habitat degradation issue increases.

⁴⁸ Chauvel, C., Dia, A. N., Bulourde, M., Chabaux, F., Durand, S., Ildefonse, P., ... & Ngounouno, I. (2005). Do decades of tropical rainfall affect the chemical compositions of basaltic lava flows in Mount Cameroon? *Journal of Volcanology and Geothermal Research*, 141(3), 195-223.

⁴⁹ Djomo, N. E., Sedláček, O., Bayly, N., Ferenc, M., Albrecht, T., Reif, J., ... & Hořák, D. (2014). Comparison of avian assemblage structures in two upper montane forests of the Cameroon volcanic line: lessons for bird conservation. *Biodiversity and Conservation*, 23(6), 1469-1484.

Altitudinal gradients

While investigating montane forests of Cameroon, I necessarily started to think about altitudinal changes. Biodiversity variation along altitude is in central focus of biogeographers and ecologists since Humboldt described in detail the gradient of Chimborazo¹. It is believed that some of the mechanisms operating behind altitudinal sorting of species are at least partly similar to those along latitude². If so, the advantage of altitude is that it has a lot of replicates around the World, which obviously does not hold for latitude. Thus, exploring elevations might assist in understanding global diversity patterns. It is true that towards higher elevations the average temperature decreases similarly as towards northern areas⁵⁰, the rainfall patterns are more variable and thus I see fewer similarities between the gradients. Annual seasonality, which is highly pronounced in extreme latitudes changes not so much along elevation. Seasonality, however, affects climatic variation within elevational bands between the tropical and temperate zone mountains, which has a crucial consequences for ecological specializations. In his seminal paper, Janzen⁵¹ suggested that tropical species are more strictly

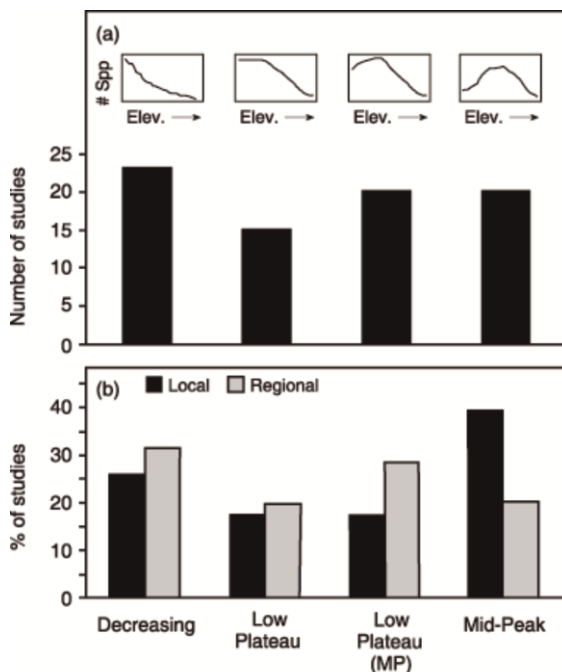


Figure 1. Four types of elevational patterns of avian species richness, adopted from McCain (2009).

confined to particular elevations as year-round stability of local conditions supports specialization, which in turn limits dispersal abilities to climatically different elevation bands. Therefore, temperate zone species occupy broader elevational ranges (note the analogy with geographical ranges) if compared to tropical ones. As a result, tropical elevational gradients are in fact steeper, and thus provide ideal model systems.

In addition, altitudinal gradients are a key to a real “ecological mystery” as they physically represent a central issue of ecology – an interaction between local and regional scales. Tropics and temperate zones differ in the composition of avifauna due to large scale biogeography. Two neighbouring forests in Europe differ in community composition due to local scale factors

such as habitat preferences of birds or migration. But the low and high elevation forests on Mount Cameroon, which are roughly 10 km apart, most likely differ due to combination of both and identify their respective importance remains a challenge. Elevational patterns in avian species richness are well

⁵⁰ McCain, C. M., & Grytnes, J. A. (2010). Elevational gradients in species richness. *eLS*.

⁵¹ Janzen, D. H. (1967). Why mountain passes are higher in the tropics. *The American Naturalist*, 101(919), 233-249.

described. McCain⁵² published a review based on almost 80 gradients around the world, from which she reduced the patterns to four principal types (Figure 1). In fact, those can be reduced even more and I see two general types: (i) declining species richness towards high elevations – this is typical for so called “humid mountains” (*sensu* McCain⁵²) with a lot of rainfall at the foothill. Mount Cameroon is a nice example of this type, (ii) hump shaped pattern with the highest richness at mid elevations – this is typical for so called “dry mountains” rising for instance from savannah such as Mount Kilimanjaro in Tanzania.

Having this in mind, I made a preliminary survey to Mount Cameroon south-western slopes in 2008, where the pristine

forest gradient occurs between 300 and 2,300 m of elevation. In 2011, I started a research project, which aimed to describe diversity pattern of birds on this poorly known mountain and make steps

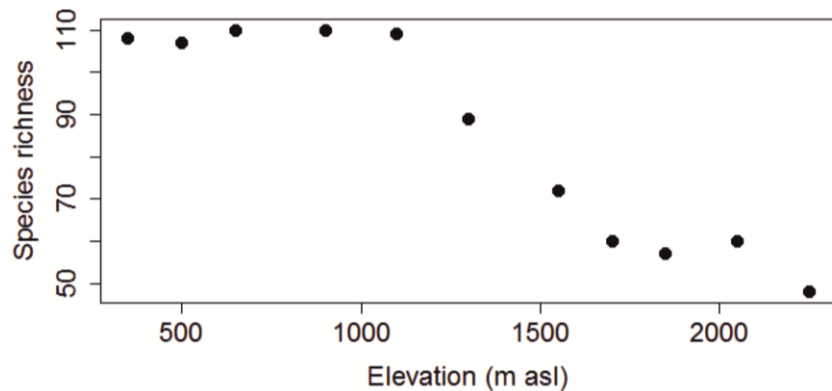


Figure 2. Pattern of species richness along elevation of Mt. Cameroon.

Our data corroborated an

expected decline in number of species towards montane areas (Figure 2). We observed the biggest change at mid-elevations around 1,100 m, where the lowland forest starts to transform to the montane one. Besides the number of species, we estimated local population densities at particular elevations by point counts. Interestingly, we found that total community abundance i.e. number of all individuals does not differ among elevations. In combination with declining species richness, we corroborated higher population densities at high elevations. Then, we tested for the shape of the abundance-range size relationship between elevational bands and revealed that in lowlands it rather fits to the positive trend predicted by the theory, which is however not the case in the upper elevations. Geographical range sizes decrease with altitude but the observed pattern in the abundance-range size relationship is mostly driven by abundances. Higher population densities at places with low species richness, specifically on islands, were described already by MacArthur et al.⁵³. They spoke about “the density compensation”. On islands, low number of species decreases the intensity of inter-specific competition, which enables the species present to maintain higher densities. It can be applied to the mountain tops as well as they serve as islands of the montane forest in the “sea” of lowland forest⁵⁴. To understand the high abundance of mountain birds more deeply, we included information about

⁵² McCain, C. M. (2009). Global analysis of bird elevational diversity. *Global Ecology and Biogeography*, 18(3), 346-360.

⁵³ MacArthur, R. H., Diamond, J. M., & Karr, J. R. (1972). Density compensation in island faunas. *Ecology*, 53(2), 330-342.

⁵⁴ Mayr, E., & Diamond, J. M. (1976). Birds on islands in the sky: origin of the montane avifauna of Northern Melanesia. *Proceedings of the National Academy of Sciences*, 73(5), 1765-1769.

elevational ranges⁵⁵ for particular species and using morphology of the mountain we were able to estimate area occupied by a species on the mountain. By incorporating population densities we then extrapolated population sizes. The subsequent analysis revealed that although montane species have higher population densities they do not differ in overall population sizes on the mountain if compared to their lowland counterparts. It implies that lower area available for montane species selects for higher population densities, which is needed for maintenance of population sizes large enough to assure survival of local (spatially isolated) population of the species. In other words, “the extinction filter” might select montane species⁵⁶. Are at the mountain tops present only those species, which were capable to maintain high population densities and thus prevented extinction in the past? Is this process supported by density compensation as described by MacArthur – smaller species pool of the mountain archipelago frees the ecological space? How does ecological specialization contribute to high abundances? Are they just a consequence of limited species pool in the mountains and available ecological space or also a result of a finer specialization of montane species? These questions remains to be tested.

Besides being abundant, montane species are different. I mean, mountains are inhabited by taxonomically specific avian species. However, are montane birds also functionally different or do montane environment select for different life-histories or ecological adaptations? Such questions open another field of my interest – how traits of birds differ along environmental gradients. Avian life histories are likely shaped by several factors – such as food limitation, predation rates or physiological constraints^{57,58}. Levels of some of these factors differ among environments, which either select for evolution of suitable life history strategies of birds living there, or enable birds bearing respective functional traits to disperse and live in such environments. Available information about elevational variation in functional traits of birds is very limited. Some papers about clutch size – the most frequently discussed avian trait – have been published. Smaller clutches at higher altitudes were reported by Badyaev⁵⁹ and seem to be a general feature of tropical high altitudes^{60,61}. Shift to slow life history in the temperate zone mountains has been reported even within species⁶². Overall the mechanisms are poorly known. Collecting detailed data about avian life history traits variation along

⁵⁵ Ferenc, M., Fjeldså, J., Sedláček, O., Motombi, F. N., Djomo, N. E., Mudrová, K., & Hořák, D. (2016). Abundance-area relationships in bird assemblages along an Afrotropical elevational gradient: space limitation in montane forest selects for higher population densities. *Oecologia*, 181(1), 225-233.

⁵⁶ Johnson, C. N. (1998). Species extinction and the relationship between distribution and abundance. *Nature*, 394(6690), 272-274.

⁵⁷ Ricklefs, R. E. (2000). Lack, Skutch, and Moreau: the early development of life-history thinking. *The Condor*, 102(1), 3-8.

⁵⁸ Ricklefs, R. E., & Wikelski, M. (2002). The physiology/life-history nexus. *Trends in Ecology & Evolution*, 17(10), 462-468.

⁵⁹ Badyaev, A. V. (1997). Avian life history variation along altitudinal gradients: an example with cardueline finches. *Oecologia*, 111(3), 365-374.

⁶⁰ Boyce, A. J., Freeman, B. G., Mitchell, A. E., & Martin, T. E. (2015). Clutch size declines with elevation in tropical birds. *The Auk*, 132(2), 424-432.

⁶¹ Freeman, B. G., & Mason, N. A. (2014). New Guinean passerines have globally small clutch-sizes. *Emu*, 114(4), 304-308.

⁶² Bears, H., Martin, K., & White, G. C. (2009). Breeding in high-elevation habitat results in shift to slower life-history strategy within a single species. *Journal of Animal Ecology*, 78(2), 365-375.

elevation of Mount Cameroon has been unfeasible until now – it requires huge field effort and knowledge of local natural conditions as well as established research site. However, at the beginning I decided to start with estimation of selection pressures potentially responsible for shaping life histories along the gradient. First, nest predation represents an important source of young mortality. Using artificial nest experiments, we tested a hypothesis that nest survival rate increases with elevation as a result of decreasing predation pressure⁶³.

Overall, elevation had no effect on the daily survival rate of the artificial nests. However, when looking at different nest types, we found that daily survival rate for cup-shrub nests decreased significantly with elevation, but for cup-ground and bareground nests, elevation had no significant effect. We further revealed that tree density, herb and shrub layer coverage, and canopy openness affected significantly the estimates of daily survival rates, which suggests that elevational changes of vegetation structure plays some role in avian nest survival. Second, we estimated parasitic load, specifically prevalence of avian malaria, in blood of birds on Mount Cameroon. This might inform about mortality risk of adults, the second crucial factor in avian life histories. The results are still unpublished, however, we found that the prevalence increases with altitude. Such a finding is somewhat contra-intuitive as more malaria was expected in lowland areas. Both abovementioned tests should be considered as preliminary as we are far from conclusions about life histories of tropical birds along elevation.

Avian clutch size

The crucial trait in avian ecology is without doubts *the clutch size*. It varies within and between species, amazing difference is observed between tropical and temperate zone species. In tropics, birds frequently lay two eggs only, while in temperate areas the clutch size rises up to four or five eggs⁶⁴. It is used as a proxy for position of a species along the slow-fast continuum of life histories, and on its variation the field of evolutionary ecology was actually set up^{65,66}. Originally, two groups of explanations have been used. First, food limitation hypothesis suggest that number of eggs in the clutch limited by amount of food, which parents are capable to bring to their offspring (“a nidifugous alternative” proposes incubation limits in bigger clutches)⁶⁶. Second, young mortality caused by nest predation limits number of eggs in the nest⁶⁷. Recently, Thomas E. Martin published a complex view

⁶³ Djomo N. E., Sedláček, O., Doležal, J., Dančák, M., Altman, J., Svoboda, M., ... & Hořák, D. (2015). Relationship between Survival Rate of Avian Artificial Nests and Forest Vegetation Structure along a Tropical Altitudinal Gradient on Mount Cameroon. *Biotropica*, 47(6), 758-764.

⁶⁴ Jetz, W., Sekercioglu, C. H., & Böhnning-Gaese, K. (2008). The worldwide variation in avian clutch size across species and space. *PLoS Biol*, 6(12), e303.

⁶⁵ Moreau, R. E. (1944). Clutch-size: a comparative study, with special reference to African birds. *Ibis*, 86(3), 286-347.

⁶⁶ Lack, D. (1947). The significance of clutch-size. *Ibis*, 89(2), 302-352.

⁶⁷ Skutch, A. F. (1949). Do tropical birds rear as many young as they can nourish. *Ibis*, 91(3), 430-458.

of the avian life history evolution⁶⁸. He observed that growth rates of tropical and temperate zone birds are comparable, however, tropical birds grow wings relatively faster. He suggests that this is favoured by predation risk and enabled by increased provisioning of individual offspring, which is constrained by nest mortality and adult effort. Thus, growth and provisioning responses to mortality explain small clutch size in tropical birds, which likely face to higher young mortality and invest more into adult survival⁶⁹.

Being a central trait in avian ecology, clutch size theory attracted a lot of my attention, too. I got field experience in clutch size variation mostly in Europe, but extremely pronounced environmental gradient in South Africa served me a study system for testing food limitation. Environmental productivity, which likely reflects availability of food for birds, is very low in western parts of South Africa and increases continually towards eastern parts, where diverse avian communities live in moist tropical savannas. I combined large scale community data based on atlas mapping with personal field experience and nest predation experiments. Firstly, I found that clutch size varies significantly across territory of South Africa, which was accompanied by variation in productivity of environment. In contrast, I found no significant pattern in nest predation risk along the gradient⁷⁰. Secondly, I went deeper into understanding of the role of food limitation in shaping clutch size. Lack's original hypothesis was later specified by Ashmole⁷¹, who pointed out that availability of food to individual birds depends on population density and that population density is limited during winter time in temperate zone birds. Therefore, the surplus of food for breeding during spring time is available for relatively low number of individuals, which thus have relatively higher amount of resources available *per capita*. This is, however, not the case in tropical regions, where lack of annual seasonality supports relatively stable population densities in the course of the year. Altogether, Ashmole suggested that annual seasonality increases clutch sizes of birds via variation in population densities. Therefore, I tested this using two explicit predictions: (i) high environmental seasonality leads to big clutches, (ii) at a given level of environmental seasonality, high maximum environmental productivity leads to small clutches, because the breeding season surplus of resources is relatively lower in such environments. I found that both predictions hold for South African bird species⁷². It thus seems that seasonality really matters for avian clutch size. Moreover, I revealed that the environmental productivity effects differ between feeding guilds. Interestingly, for insectivorous and frugivorous birds I observed the expected patterns, however, I did not find a support for them in granivorous

⁶⁸ Martin, T. E. (2015). Age-related mortality explains life history strategies of tropical and temperate songbirds. *Science*, 349(6251), 966-970.

⁶⁹ Wiersma, P., Muñoz-García, A., Walker, A., & Williams, J. B. (2007). Tropical birds have a slow pace of life. *Proceedings of the National Academy of Sciences*, 104(22), 9340-9345.

⁷⁰ Hořák, D., Sedláček, O., Tószögyová, A., Albrecht, T., Ferenc, M., Jelínek, V., & Storch, D. (2011). Geographic variation in avian clutch size and nest predation risk along a productivity gradient in South Africa. *Ostrich*, 82(3), 175-183.

⁷¹ Ashmole, N. P. (1963). The regulation of numbers of tropical oceanic birds. *Ibis*, 103(3), 458-473.

⁷² Hořák, D., Tószögyová, A., & Storch, D. (2015). Relative food limitation drives geographical clutch size variation in South African passerines: a large-scale test of Ashmole's seasonality hypothesis. *Global Ecology and Biogeography*, 24(4), 437-447.

species. Those feed their young with insects but outside the breeding season they can utilize resources from the seed bank and thus the population limitation during the period with low food supply might be less pronounced in this guild. In a similar analysis on European birds, we found that clutch size is higher in more productive (higher NDVI) and seasonal environments and corroborated that longer breeding season contributes to reproductive effort by increased number of breeding attempts⁷³. However, the observed patterns differed between precocial and altricial species.

Analysis of clutch size opens a question of the links between different avian specializations. Life history traits are often correlated and specialisation for one particular resource can limit or direct variation in others⁷⁴. It follows from above that feeding specialization influences reproductive investment. Ricklefs & Wikelski⁷⁵ argued that individual adaptive responses to different environments are limited by physiological mechanisms, namely that endocrine control mechanisms produce incompatible physiological states that restrict variation in life-histories. Indeed, hormonal levels were identified as correlates of crucial life history traits in birds⁷⁶. Besides, habitat specializations influence the traits of birds. This is a crucial issue in functional biogeography – the field of my interest, which describes geographical patterns in ecological traits. Such patterns can be theoretically created by several processes but there are two important related to habitat, which obviously work simultaneously: (i) traits evolve under environmental conditions of a particular place, (ii) environmental conditions of a particular place filter the species present according to the traits they already bear (environmental filtering)⁷⁷. In avian evolutionary history, habitat occupied or way of its use obviously influenced evolution of phylogenetically conservative morphological traits such long legs in waders, inter-digital webbing in ducks or x-shaped zygodactyl leg in Piciformes. Links between morphology and habitat have been described a part of the process of niche differentiation between closely related species, typically the genus *Acrocephalus*⁷⁸. Besides, the rate of habitat specialization might reflect in other ecological traits of birds. In a recent paper⁷⁹, we tested the links between habitat specialization and some other ecological traits in European birds. We decided to perform such an analysis across European territory first as it offers better distributional and habitat preference information at continental scale if compared to Africa. However, similar analysis can be done in the future on subsets of African birds such as those living in South Africa. Such a comparison might be informative as European environments are more affected by human activities. Anyway, we found that habitat

⁷³ Kopsová-Storchová, L., Storch, D., Brotons, L. and Hořák, D. (2017), Geographical Variation in Reproductive Investment across Avian Assemblages in Europe: Effects of Environmental Drivers Differ Between Altricial and Precocial Species. *Journal of Avian Biology*. Accepted Author Manuscript. doi:10.1111/jav.01131

⁷⁴ Stearns, S. C. (1989). Trade-offs in life-history evolution. *Functional ecology*, 3(3), 259-268.

⁷⁵ Ricklefs, R. E., & Wikelski, M. (2002). The physiology/life-history nexus. *Trends in Ecology & Evolution*, 17(10), 462-468.

⁷⁶ Hau, M., Ricklefs, R. E., Wikelski, M., Lee, K. A., & Brawn, J. D. (2010). Corticosterone, testosterone and life-history strategies of birds. *Proceedings of the Royal Society of London B: Biological Sciences*, 277(1697), 3203-3212.

⁷⁷ van der Valk, A.G. (1981) Succession in wetlands: a Gleasonian approach. *Ecology*, 62, 688–696.

⁷⁸ Leisler, B., Ley, H. W., & Winkler, H. (1989). Habitat, behaviour and morphology of *Acrocephalus* warblers: an integrated analysis. *Ornis Scandinavica*, 181-186.

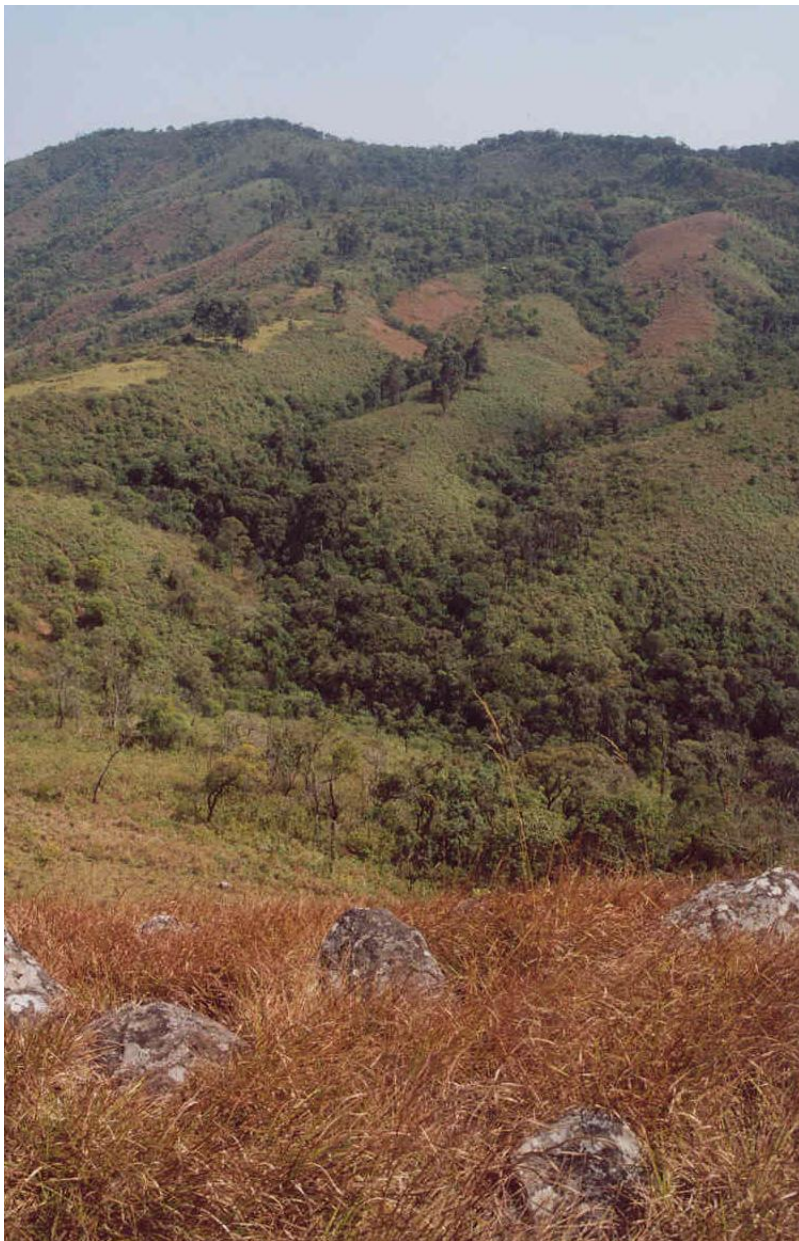
⁷⁹ Reif, J., Hořák, D., Krištín, A., Kopsová, L. and Devictor, V. (2016), Linking habitat specialization with species' traits in European birds. *Oikos*, 125: 405–413.

specialists had narrower diet niche, wider climatic niche, higher wing length/tail length ratio and migrated on shorter distances than habitat generalists. Our results support an expected positive link between habitat and diet niche breadth estimates and corroborated that habitat specialization reflects occupation of morphological space, when specialists depend more on manoeuvrability of the flight and are thus more closely associated to open habitats than habitat generalists. It implies that habitat specialists occur mostly in spatially restricted environments with high climatic variability such as mountain areas. Finally, our results indicate that long distance movements might hamper narrow habitat preferences.

In conclusion, my research endeavours to reveal whether and how ecological specializations matter for species richness patterns. As an explicit theoretical framework is missing for many aspects of this issue, to get more insight, so far I combined descriptive work with testing of particular hypotheses, which brought interesting results about links between spatial variations in traits, number of species and the environment. I think, the future work in this respect should be directed on (i) development of a relevant theory, which will provide a base for subsequent data collection and hypotheses testing; the ecological specializations are in contemporary theories are frequently included only implicitly (ii) surveys of tropical environments, where the role of ecological specializations is presumably more pronounced due to temporal stability of climate, (iii) still more detailed work on elevational gradients as they combine local and regional effect on distribution of diversity, (iv) concrete comparisons between tropical and temperate regions might further elucidate, how tropical mechanisms are changed in relatively younger temperate zone systems.

Chapter 1

Hořák, D., Sedláček, O., Reif, J., Riegert, J., & Pešata, M. (2010). When savannah encroaches on the forest: thresholds in bird–habitat associations in the Bamenda Highlands, Cameroon. *African Journal of Ecology*, 48(3), 822-827.



Chapter 2

Reif, J., **Hořák, D.**, Sedláček, O., Riegert, J., Pešata, M., Hrázský, Z., Janeček, Š. & Storch, D. (2006). Unusual abundance–range size relationship in an Afrotropical bird community: the effect of geographical isolation? *Journal of Biogeography*, 33(11), 1959-1968.



Chapter 3

Djomo, N. E., Sedláček, O., Bayly, N., Ferenc, M., Albrecht, T., Reif, J., Motombi , F. N. & **Hořák, D.** (2014). Comparison of avian assemblage structures in two upper montane forests of the Cameroon volcanic line: lessons for bird conservation. *Biodiversity and Conservation*, 23(6), 1469-1484.



Chapter 4

Ferenc, M., Fjeldså, J., Sedláček, O., Motombi, F. N., Djomo, N. E., Mudrová, K., & **Hořák, D.** (2016). Abundance-area relationships in bird assemblages along an Afrotropical elevational gradient: space limitation in montane forest selects for higher population densities. *Oecologia*, 181(1), 225-233.



Chapter 5

Djomo N. E., Sedláček, O., Doležal, J., Dančák, M., Altman, J., Svoboda, M., Majeský, L. & **Hořák, D.** (2015). Relationship between Survival Rate of Avian Artificial Nests and Forest Vegetation Structure along a Tropical Altitudinal Gradient on Mount Cameroon. *Biotropica*, 47(6), 758-764.



Chapter 6

Hořák, D., Sedláček, O., Tószögyová, A., Albrecht, T., Ferenc, M., Jelínek, V., & Storch, D. (2011). Geographic variation in avian clutch size and nest predation risk along a productivity gradient in South Africa. *Ostrich*, 82(3), 175-183.



Chapter 7

Hořák, D., Tószögyová, A., & Storch, D. (2015). Relative food limitation drives geographical clutch size variation in South African passerines: a large-scale test of Ashmole's seasonality hypothesis. *Global Ecology and Biogeography*, 24(4), 437-447.



Chapter 8

Kopsová-Storchová, L., Storch, D., Brotons, L. & **Hořák, D.** (2017). Geographical Variation in Reproductive Investment across Avian Assemblages in Europe: Effects of Environmental Drivers Differ Between Altricial and Precocial Species. *Journal of Avian Biology*, in press.



Chapter 9

Reif, J. & **Hořák, D.**, Krištín, A., Kopsová, L., Devictor, V. (2016): Linking habitat specialization with species' traits in European birds. *Oikos*, 125: 405–413.

