Chapter 1 **Introduction: Studying Birds in Time** and Space



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Abstract Birds are of high public interest and of great value as indicators of the state of the environment. Some 11,000 species are a number relatively well to handle. From a scientific point of view, it is not easily answerable what a species is, since speciation and extinction are ongoing evolutionary processes and differentiation among species works on various traits. Contemporary systematics attempts to take into account as many criteria as possible to delimit species. The currently most influential approach is the use of genomic sequences, be it as a neutral marker or to discover the underpinnings of functional traits. The study of the outer appearance of birds nevertheless remains fundamental, since that is the interface between a bird and its biotic and abiotic environment. For the majority of bird species, acquired traits of vocal communication add to this complex. Birds can also vary the timing of important behavior such as breeding or molting. Most fascinating among circannual behavior are the long-distance movements that can quite fast evolve and have genetic bases. Despite such dispersal ability for many bird species, geographic barriers play a large role for distribution and speciation in birds. Extant, former, and potential future ranges of a species can be modeled based on the abiotic niches individuals of this species have. Within a species' range, genetic and phenotypic traits vary and promote to process toward species splits. Beside geographic frameworks, ecological circumstances play a major role and contribute to natural selection but also trigger individual responses such as phenotypic plasticity, modification of the environment, and habitat selection. Anthropogenic global impacts such as climate and land-use changes (e.g., urbanization) force extant species to accelerated modifications or population splits or let them vanish forever. Only if humans leave more room and time to birds and other organisms can we expect to maintain such a number of diverse bird species, although they will keep modifying, splitting, and becoming extinct—but for natural reasons.

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1.1 Why and How to Study Bird Species

For many people around the world, birds are among the most fascinating fellow animals on Earth. Ornithology, the scientific study on birds, is one of the oldest organized scientific disciplines (Birkhead et al. 2014). And birds are among the best studied organisms (del Hoyo et al. 1992–2013). So why are we presenting yet another book on birds and especially bird speciation?

What we nowadays recognize as a bird is the relatively small-sized feathered survivor of the dinosaur assemblage of reptiles. These warm-blooded vertebrates diversified into tens of thousands of species within the last 150 and especially 65 million years. And while this diversification process keeps going, species have become extinct—for natural and increasingly for non-natural reasons. While there are many ways how we humans are letting the numbers of bird individuals and species diminish, there is also a lot we could and should do to halt this trend and preserve avian diversity.

To that end—and for many scientific reasons—it is important to understand what a bird species is and how it arises, is modified, and vanishes. It is far less easy than it appears to circumscribe a bird species. This is mainly due to the transient nature of species. Being one descendant of another species, a species can slowly become another species (anagenesis), die out, or split into two or more daughter species (cladogenesis).

In the 2000s, Newton (2003) and Price (2008) summarized the state of knowledge on this last aspect, which is so fundamentally important for the generation of bird diversity or biodiversity in general. A lot of advancement has been achieved since then, be it in the field of genomic foundations of species, bird distributions and their modeling, or (macro)ecological insights. And on the downside, human impact through land-use and climate changes has challenged more and more bird species and also reduces the population sizes of hitherto abundant species.

That is why publisher and editor both wished to compile an update on the topic of bird speciation but also to widen the audience from specialists to general bird enthusiasts and conservationists. A variety of experts—from PhD students to senior researchers—elaborate on various aspects in the following chapters.

George Sangster starts with the timely approach on how to circumscribe or even define a bird species (Chap. 2). Instead of using a fixed degree of differentiation in a certain genetic marker or some other scoring, he favors an integrative synopsis of as many lines of evidence available for the birds in question such as morphology, genetics, distribution, and behavior. This does not make things easier but proved to be most adequate.

We wish to keep your confusion as little as possible when diving deeper into bird species mysteries and follow the taxonomy and nomenclature of birds according to the IOC World Bird List version 7.1 (Gill and Donsker 2017, worldbirdnames.org) throughout. In contrast to other such comprehensive bird species lists, this global endeavor has scientific reasoning as first priority and works on a peer-reviewing basis. Since this meets the spirit of the time most, scientific societies such as the British Ornithologists' Union (BOU) and the German Ornithologists' Society (DO-G) decided to trust this expert panel and save the human resources in their own ranks from evaluating updates in bird systematics.

Although species delimitation should not rely on any single method alone, the study of the molecules of life, especially DNA, let research in this field make a huge leap forward three decades ago (Sibley et al. 1988). Progress in this field accelerated, and whole genomes have now become the focus (Ellegren 2013). The B10K project (https://b10k.genomics.cn) is ambitiously attempting to assemble genomic data for all known bird species. It kicked off at the level of bird orders (Jarvis et al. 2014).

Most chapters will cite work that has at least incorporated research on molecular markers. Daronja Trense and I thus provide some basic knowledge about how the genetic information of birds is organized, used by the birds themselves and by researchers who want to understand evolutionary changes and differences between individuals as well as between taxa on higher levels (Chap. 3). This chapter is mainly written for readers without training in biology, but due to the fast development in molecular biology, it might offer interesting updates for biologists who graduated more than few years ago.

1.2 Physical and Behavioral Aspects of Birds

Phylogenies based on genome sequences might provide the "backbone" for further studies, but variability at the molecular level is not necessarily detectable in the individual birds and their phenotypes. So whatever we observe as outer appearance or behavior (e.g., vocalizations, temporal changes, migration) are the characteristics that are also perceived by conspecifics and other animals as well. They constitute the phenotype on which selection works, and thus they are also very important to gain understanding for species and speciation.

Till Töpfer shows that the morphological variability within and among bird species can have many reasons such as sexual dimorphism, changes during an individual lifespan, adaptation to local environmental conditions or rather short-term reactions to environmental influences (phenotypic plasticity) (Chap. 4). He also presents several methods to describe structural or measure two- or three-dimensional features of a bird and emphasizes the importance of public bird collections that allow for robust comparative studies.

While morphological traits are mostly inherited, be it under the interplay of several genes, bird behavior, specifically song, can have some learning component. This adds cultural evolution as another driving force for bird species diversity and

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makes birds also models for the study of the evolution of human language. Martin Päckert introduces the three major bird clades that are capable of learning their song which plays an important role in species recognition and sexual selection (Chap. 5). They together comprise 54% of the 10,828 bird species recognized in this book (Gill and Donsker 2017). Similar to the advancement in genetic studies, bioacoustic methods such as sound recording in the field and sonagraphic analysis on screen have allowed for new insights in bird behavior and species delimitation.

Singing and other vocal behavior are controlled neuronally as well as hormonally and occur at specific times of the day and of the year. Barbara Helm and Robyn Womack describe some examples for timing in birds and demonstrate how different timing of breeding alone can lead to species divergence (Chap. 6). If breeding time is an inherited trait, then all descendants of an "innovative" breeding pair will keep to this alternative time and not form pairs with "traditional" conspecifics.

One of the most fascinating phenomena we observe in birds is their migratory behavior, i.e., seasonal movements, mostly between breeding areas and some sort of maintenance range(s) outside the breeding season. This is another example of an annual rhythm, with additional aspects to consider including navigation and the buildup of fat deposits. The when and where to of bird migration has to be adapted or adjusted to climatic changes and food availability. Such behavioral traits are thus quite labile. Nevertheless, they can be studied on both micro- and macroevolutionary levels. Miriam Liedvogel and Kira Delmore provide an overview on important aspects of bird migration within the scope of our book, report state-of-the-art genomic studies to understand the regulation of this behavior, and show how migration might play a role in the speciation process (Chap. 7).

1.3 The Spatial Component

For the diversification of birds, geography has been most important. Manuel Schweizer and Yang Liu demonstrate for major basal lineages of birds how they apparently arose before the background of continental drift (Chap. 8). The majority of bird species are able to fly and manage to disperse to hitherto uninhabited areas, before they become extinct in the current range. Such exchange between two areas can become impossible over time when barriers such as mountains or rivers grow. If the separated populations remain on their own for sufficient time (in allopatry), they might become reproductively incompatible and do not interbreed upon secondary contact. And if they also diversify in ecological respect so that their ecological niches do not overlap too much, they can also live in the same area (in sympatry) and their ranges overlap instead. For historical reasons as well as due to gradients in environmental resources across the Earth, the number of bird species varies a lot across space.

Within a certain timeframe, the ecological niche of a bird species remains quite stable and might also be inherited by daughter species (niche conservatism). Nevertheless, niches of sister species have to diverge to allow range overlap. Darius Stiels and Kathrin Schidelko explain how avian niches can be characterized based on the abiotic features under which we find representatives of extant species (Chap. 9). This approach allows researchers to model the (potential) distribution of a taxon now, in the (recent) past, and the—very near!—future (under various climate change scenarios or for cases of species introductions).

Finally, Leo Joseph elaborates from not only, but a more Australian perspective how intraspecific genetic differences lead to observable patterns and potentially to allospecies, geographically separated (young) species (phylogeography) (Chap. 10). Upon secondary contact, these taxa—no longer subspecies, not yet full species—may still exchange genetic information and even produce an intermediate taxon by such hybridization. Various genetic markers and phenotypic traits may or may not resolve the same pattern and elucidate or rather blur the current stage of the respective populations on the speciation trail. In consequence, we need to accept that any bird population is rather a continually evolving evolutionary lineage than a permanent species or subspecies.

1.4 Ecology Matters: Bird Species in the Anthropocene

In contrast to allopatric speciation emphasized so far, it has in the recent past become clearer and clearer that also in birds various ways of sympatric speciation can be found. Pim Edelaar elaborates on various modes of ecological speciation in birds: natural selection, phenotypic plasticity, adjustments of the environment, and habitat selection (Chap. 11). Foremost, individuals in a given population that have more suitable trait states for the area and habitat they live in right now have higher chances to survive and to produce a higher number of offspring (i.e., being fitter in the evolutionary sense = Darwinian natural selection). On a smaller temporal scale, individuals react to challenges within their lifetime within the framework of their inherited constitution (phenotypic plasticity), and this may nevertheless lead to segregation within the population. Regarding the bird's environment, they can actively make it more suitable for their phenotype by either modifying their surroundings or moving to areas better for foraging or nesting than the current one. Again, if only part of the population chooses to react that way, it might split in the long run.

The two final chapters deal with two major anthropogenic threats to bird-species diversity: climate and land-use change. Neither is completely "new" to birds, because both climate and surface structure have changed tremendously over the history of the Earth. But in the Anthropocene, these changes have occurred (almost) globally and so quickly that many species cannot maintain their population sizes, range extents, and/or genetic diversity.

We are well aware of the fact that increased output of certain gases by human activities (CO_2 emissions increased by 62% from 1992 until 2016 alone; Ripple et al. 2017) has intensified the generally necessary greenhouse effect and not only raised the average temperature on Earth (by approx. 0.5 °C from 1992 until 2016 alone; Ripple et al. 2017) but also consequently triggered various other climatic effects. A vast body of literature has accumulated that describes, models, and interprets the impact of these climatic changes on birds (and other organisms). And indeed, birds

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are affected in many ways: timing of migration and breeding have been adjusted, population sizes changed, ranges shifted, population and community compositions altered. Sven Trautmann summarizes approaches and findings as well as potential consequences for bird species conservation (Chap. 12).

Among the many changes of land use humans perform, the building of our own homes in relatively high density is a very striking example with severe consequences for birds. Caroline Isaksson provides numerous examples for urbanization impacts on birds (Chap. 13). While some species (urban exploiters) even profit from the environmental conditions humans create in cities, urban adapters are somehow able to live in human settlements but suffer from certain restrictions and might exhibit lower survival rates and fecundities than their rural conspecifics. Finally, species that are too shy or too specialized on habitats not found in cities (urban avoiders) get their ranges reduced in overall size, fragmented, and disconnected. While the latter has population-genetic effects and might lead to allopatric speciation in the long run, the coexistence of urban and rural populations of a single species has at least vast phenotypic consequences at the extent of what has naturally occurred over much longer time.

As a consequence of the insights into (natural) speciation processes and (anthropogenic) constraints on bird life these days, we need to reflect on traditional bird conservation strategies and ask if they sufficiently take into account the pervasiveness of human impact. Consequences of human action can be found globally and do not spare nature reserves (protected or even managed with a lot of effort) on the one hand and that birds on the other hand—as most living beings—adhere to intrinsic and extrinsic evolutionary "rules" that make it impossible to preserve a given "species" forever.

(Bird) species arise, modify, and vanish. If we want to protect "nature"—as a cultural ethic value—in its diversity and the birds we love for various reasons, we need to prevent their extinction and allow them to change, but in their way and speed. Therefore, we have to provide them sufficient space and time. Space: Restrict human settlements to far less than 100% of the continental surface (and marine space) and abandon developmental goals that promise optimal (urban or even metropolitan) living conditions to each human and every remote village. Time: Slow down or even reverse environmental impacts such as greenhouse effect, pollution, and land-use changes.

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I had gained some overview of the topic during my doctoral studies with Jochen Martens and postdoctoral research with Trevor Price and Michael Wink.

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