

Systematics, population genetics, and taxonomy, and their importance for tracking

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ABSTRACT: The process of evolutionary divergence produces a populations-subspecies-species-genus (etc.) continuum of differentiation. The fields of population genetics and systematics study patterns and processes from opposite ends of this divergence continuum, and taxonomy describes, names, and classifies the results of these studies. New methods of assessing population characteristics in phenotype and genotype, and new analytical methods, are improving our ability to determine where populations lie along the divergence continuum and their relationships and degrees of uniqueness. New techniques are also enabling us to more fully describe avian diversity, but genomic techniques in particular are furthering our understanding of how lineages responded to past climatic changes. As we learn more about evolutionary histories of lineages at the species level and below, we are finding more that we need to pay attention to as important components of biodiversity (e.g., evolutionarily significant units, subspecies, and some phylogenetic species). We still have much work to do to fully describe extant avian diversity so that we know which populations we should be tracking when monitoring change. We should include a specimen component in our monitoring programs to enable future retrospective studies, which are proving invaluable for understanding recent historical changes in birds and our shared environments.

DURING THIS ERA of profound global change, we are also witnessing revolutions in population genetics, avian systematics, and taxonomy (see glossary). Technological and conceptual advances are helping us understand avian diversity and relationships better than ever before, causing rapid taxonomic changes throughout the class Aves, from the shallowest to the deepest levels (subspecies to orders; e.g., Fjeldså 2013, del Hoyo and Collar 2014, Jarvis et al. 2014). How do we relate these changes in our understanding of birds to understanding and managing the effects of global change on these birds? And how might the tools being used to understand avian diversity also be used to more effectively maintain that diversity? This review will outline some of the important factors that help answer these questions. Few of the answers are simple, and we can expect ongoing changes, but several key parameters are relatively stable: the evolutionary process of divergence, the principles of population genetics, and global change.

Evolutionary divergence and speciation

The divergence process begins when one population becomes two (or more) and differences begin to accumulate between them. These differences can be affected by selection (natural or sexual) or be evolutionarily neutral. Most genetic changes are neutral or nearly neutral, because most DNA mutations do not affect phenotype (including altering amino acid coding; Kimura 1983, Ohta 2002). Phenotype is under selection, so we tend to consider most phenotypic variation as non-neutral (excluding traits subject to cultural evolution, e.g., some behaviors). Relationships between genotype and phenotype are complex, and a lot of research is being done in areas such as developmental processes, environmental effects, gene regulation, epigenetics, and phenotypic plasticity to better understand them. Most of our data on avian diversity, however, are phenotypic and genotypic, and it is useful to portray evolutionary divergence as a simple, two-dimensional process along these two

different divergence axes (Fig. 1).

Exactly where a population, subspecies, or species lies in this divergence space (Fig. 1), in relation to its closest living relative, can be difficult to determine. Not only does our understanding tend to improve with more data, but conceptual issues can lead to different interpretations of those data. For example, multiple species concepts were proposed in the 20th century (Coyne and Orr 2004), affecting where different practitioners draw a line between two lineages being species or not. In ornithology, the biological species concept prevails, and this is likely to continue because of difficulties in applying evolutionarily meaningful thresholds other than reproductive isolation, which does not need to be complete (more on gene flow below). But even applying the criterion of reproductive isolation is difficult, particularly among allopatric (geographically separated) populations.

Speciation is usually considered to be a protracted process, and lineages that begin the divergence process may never achieve speciation (Mayr 1969, Coyne and Orr 2004, Price 2008). In birds, the speciation process ranges over two orders of magnitude in time; it can be relatively quick, on the order of tens of thousands of years, or it can drag on for very long periods, e.g., >1,000,000 years (Price 2008). Time alone is therefore not a very useful measure of species limits, probably because speciation is driven largely by selection, which is of course highly variable among populations and lineages.

The question of whether or not a group of organisms is best considered a species has generally been answered either directly or by inference using a comparative method. This approach examines what occurs between lineages at contact zones (i.e., directly) or, if such contact zones do not exist, what happens between other, closely related lineages when they are in contact (i.e., by inference; Mayr 1969, Mayr and Ashlock 1991). The general approach is that we determine that it

takes “about this much” difference between lineages to result in reproductive isolation when the animals have the opportunity to mate with each other, and we then apply that “about this much” threshold to other lineages in closely related groups, particularly among allopatric populations (i.e., a measured degree of difference between lineages that are clearly species is used as a proxy when two lineages’ status is uncertain). For numerous reasons this approach has been dominated by phenotypic data. Historically this has not been an exact science, but the approach has been very effective in zoology for categorizing diversity (e.g., Remsen 2005). Tobias et al. (2010) have introduced a quantitative phenotypic approach to these analyses for all birds using the statistics of effect size (Mayr 1969, Patten 2010). While this represents an important advance, particularly in making diagnoses more transparent, it is not perfect (Winker 2010) and its first broad implementation (del Hoyo and Collar 2014) is generating considerable controversy (Remsen 2015). Where to draw a line between species and not-species is very difficult in many cases, but an understanding of population genetics can help.

Population genetics

Classic views of speciation considered that only allopatric populations could become reproductively isolated and thus become separate species. A rapidly growing body of evidence is showing that speciation can also occur with small amounts of gene flow still occurring (Feder et al. 2012, Nosil 2012, Turelli et al. 2013). Ornithologists have long known that species-level lineages could withstand some levels of gene flow between them. The many species of *Anas* ducks, for example, maintain their species status despite frequent examples of interspecific hybrids (see also Grant and Grant 1992). But gene flow cannot be treated simply as a presence/absence phenomenon; there are three important aspects: 1) The effects of gene flow are highly nonlinear

(Wright 1943, 1951; Cabe and Alstad 1994; Mills and Allendorf 1995; Fig. 2). 2) Small amounts of gene flow can be beneficial, e.g., by diminishing the negative effects of inbreeding or enabling new adaptation to occur (Slatkin 1987, Morjan and Rieseberg 2004, Räsänen and Hendry 2008). 3) Small amounts of gene flow can retard adaptation and divergence, even under strong divergent selection (Slatkin 1987, Rice and Hostert 1993, Hostert 1997, Lenormand 2002, Postma and van Noordwijk 2005).

Isolated populations can become genetically diagnosable relatively quickly through mutation and genetic drift, particularly at small population sizes, when the effects of drift are accelerated. For example, if a hypothetical population is divided into three subpopulations, of sizes large, medium, and small, and no change occurs in the selection regime, the smallest subpopulation will accumulate diagnosable genetic differences fastest simply because of its size. Is that evolutionarily significant? Probably not at the level we wish to focus on in management and conservation. Do we want to call this subpopulation a species because it has become genetically diagnosable? Probably not with those data alone. Are these genetic differences important? They are evolutionary events, and their presence can help us understand things such as degree of (and by inference time since) divergence, genetic diversity, and historical demographic parameters such as effective population size (N_e) and gene flow. But in this simple conceptual model these differences are driven mostly by the stochastic process of drift, which is not considered to be the primary driver of speciation.

Instead, selection is considered to be the most important factor in speciation (Coyne and Orr 2004, Price 2008), leading us to ask whether or not differences are evolutionarily important, e.g., neutral or non-neutral. We usually look to phenotype for indications of divergence that is “important” in an evolutionary sense. Thus, in birds, plumage color or pattern, vocalizations, and behavior are often used as indicators of whether or not lineages have diverged sufficiently to be

considered species. We use these character suites because we can see that the birds themselves respond to them, which in turn affects assortative mating and gene flow. So genetic diagnosability alone is not a particularly useful criterion for diagnosing species (more on this below), but it can stimulate us to integrate genotypic and phenotypic data to better understand the nature of the divergence (Winker 2009).

Three more things should be kept in mind when interpreting population genomic data: 1) Below the species level, we should expect to frequently encounter discordant signals between genetic and phenotypic datasets and even among different genetic datasets (e.g., Winker 2009, Humphries and Winker 2011). 2) Geography alone, in the absence of any additional factor (e.g., no barriers to gene flow), can affect the distribution of genetic variation and potentially cause three phenomena: isolation by distance (IBD; Wright 1943), random phylogeographic breaks (Irwin 2002), and a center-of-range increase in genetic diversity through geometric constraints on gene flow (Miller et al. 2010). 3) It is important to understand that most phenotypic traits are polygenic; the historical one-gene, one-trait concept has mostly died out because the phenomenon is rarely encountered (e.g., Shapiro et al. 2013). Literally hundreds, and perhaps even thousands, of loci can influence a trait such as human height (Wood et al. 2014).

Applications of these principles

Over the past decade there has been tremendous growth in species delimitation methods using genetic and genomic data (Carstens et al. 2013). Champions of the wave of coalescent methods (see glossary) for species delimitation are excited about the increased ability to find evolutionarily independent lineages (e.g., Fujita et al. 2012). It is indeed wonderful to apply these new tools to discover and study lineages to answer diverse questions. *But evolutionary independence is not*

equivalent to speciation. A few generations of isolation (e.g., through colonization or a separation event such as through habitat loss) can cause a population to be evolutionarily independent. While evolutionary independence can be an important part of speciation, when used alone these new methods are weak for species delimitation for one or more reasons. For example, most of the signal in the data is neutral or near-neutral; that signal is strongly affected by effective population size; gene flow is usually not accounted for; these analyses are strongly affected by sample size (individuals and loci) and especially sample distribution; and phenotype and the actions of selection are often excluded from analyses. These new methods would be more accurately termed “lineage delimitation,” and, importantly, lineages can span the entire divergence continuum.

Because we humans are a vertebrate species with geographically partitioned variation, it helps to look at ourselves as a well-studied species to see where things are likely headed. Three examples in particular show just how sharp a tool genomic surveys can be. The diagnosability of the human population of Helsinki, Finland, from other European populations is remarkable in Lao et al. (2014) using their GAGA algorithm. Even more remarkable, perhaps, is the ability of Xing et al. (2009) to distinguish between upper- and lower-caste Indians “despite being sampled from the same geographic location, speaking the same language, and having a relatively small [genetic] distance from each other...” There are phenotypic correlates in both of these cases, i.e., language and social behavior. Finally, O’Dushlaine et al. (2010) showed high levels of genetic structure (89-100% diagnosability) among European villages just 8-30 km apart.

My premise here is simple, but very important: genomics alone cannot be used to reliably define species or subspecies. The power of these tools and datasets to effectively diagnose groups or lineages all along the divergence continuum (populations—evolutionarily significant units—subspecies—species—genera, etc.) precludes their ready application for placing a lineage or group into

a particular category. The problem lies in converting evidence of divergence and a measurement of this divergence into explicit categories. We would need to define multiple new (and somehow congruent) thresholds of divergence among heterogeneous datasets to denote what equals subspecies, species, etc., and these data and definitions would still be without much connection to evolutionary selection. Instead, we need to integrate phenotypic and genotypic datasets, as most taxonomists already do (Winker 2009, Carstens et al. 2013) and use comparative methods to understand what groups or lineages belong in which of each of the categories we use to denote stages along the divergence continuum.

Each year brings increased power in diagnosing smaller and smaller groups, often with amazing accuracy. Such “diagnosably distinct” units will not all warrant recognition as species or subspecies, and this is where taxonomic categories meet other important, finer-scale categorical bins on the divergence continuum, such as evolutionarily significant units, distinct population segments, and management units. With such levels of fine-scale signal present in large genomic datasets, lineage delineation can become a rather trivial exercise unrelated to species, subspecies, or anything of evolutionary importance. Also, with such signal available in genomics studies, ultimately it probably doesn’t matter what analytical methods are applied (although we should apply multiple methods and seek congruence; Carstens et al. 2013). What does matter is that we recognize that lineage or group diagnosability using genomics is not equivalent to any specific categorical bin on the divergence continuum. As genomic data sets accumulate, we will see this simple fact slowly being worked out as we collectively incorporate key principles such as the huge component of neutral, random processes in genomic data. Coupled with sampling error (in how we sample the genome and in the numbers and distributions of the animals we include in our studies), there is and will continue to be considerable confusion. We’re probably still in early innings here, so there will be

years of disagreement ahead, even among experts.

To approach this from another perspective, consider a genotype (i.e., allele or haplotype) that is at a very high frequency or perhaps even fixed in a population. Examples include lactase retention in adult humans, which reaches high frequencies in western European populations (Gerbault et al. 2011) and some of the alleles affecting human pigmentation (Sturm and Duffy 2012). Strong selection that pushes an allele to high frequency or fixation in a population does not make a species, regardless of whether gene flow connects populations. Such selective sweeps are not speciation events; let's not confuse adaptation with speciation. Fixation through genetic drift is also not speciation (and distinguishing between drift and selection can sometimes be intractable; Hughes 2007, Bank et al. 2014). Single-locus perspectives on speciation can be wrong (e.g., the phylogenetic tree of a gene can mismatch that of species—'gene trees do not equal species trees'; Avise and Wollenberg 1997, Degnan and Rosenberg 2006), and in fact they will often be wrong at very shallow evolutionary levels, particularly when considering how many alleles track population splits at these levels. Some of the alleles that track certain splits will be helpful in the future in reconstructing speciation history in a lineage (systematics), but at present most of these ubiquitous population genomic events, scattered widely and in very high numbers across the genome, will mean little or nothing.

Both in evolutionary research and in conservation (e.g., USD I and USDC 1996, COSEWIC 2005), subspecies will continue to demand our attention. This topic has been extensively debated, particularly in relation to species concepts (Winker and Haig 2010). Most practitioners probably agree that there is geographically partitioned variation, and that some of this variation falls below the level of species, regardless of the species concept applied. One could argue that the debates revolve mostly around how we treat (nomenclaturally) and what we do with (manage) geographically

partitioned variation within species, regardless of whether that variation is genetic or phenotypic. And it should be re-emphasized that the validity of described subspecies cannot be reliably tested using genetic data; there are reasons to expect discordant signal between phenotype and genotype at such shallow evolutionary levels (Winker 2009; Patten 2010, 2015). Subspecies remain important, although not to everyone.

There is a significant issue here also of local adaptation. We should value subspecies or any other form of heterogeneously distributed phenotypic variation as the sort of diversity that enables species lineages to be resilient and to be retained through times of environmental change. Some aspects of genetic variation are important here as well (Hoffman and Sgrò 2011, Brooks et al. 2015), although separating neutral from adaptive variation can be difficult. As a simple example, consider that future environmental conditions include only a subset of current conditions, as well as novel conditions, leaving today's populations that are outside of that future set threatened with extinction. Presently, we do not have a lot of predictive power over how future environmental envelopes relate to present ones (e.g., the size and nature of overlap) or what biodiversity we should be managing to minimize extinction risk. This makes intraspecific variation (e.g., subspecies, or geographically partitioned adaptive genetic variation) particularly valuable because it occupies a wider range of current environmental conditions, increasing the likelihood of some of it being in that overlap zone with future conditions and thus preventing species-level extinction. If we are to successfully manage species lineages, maintaining within-species diversity improves our odds—in practical terms, a shotgun approach to hitting a difficult evolutionary target.

Changes within lineages

Although systematics and taxonomy usually evaluate and categorize relationships among

lineages, important changes occur within a lineage independently of its relationship(s) to other lineages. We tend to think more often in terms of profound changes over long periods of time (macroevolution), in which different species names may be applied to morphotypes as a lineage's phenotypes change through time (anagenesis; e.g., *Homo erectus* versus *H. sapiens*). But within-lineage changes and the potential for them are very important for lineage retention in the short term (microevolution), and with respect to global change we need to recognize that sometimes changes can occur relatively rapidly, in birds and other taxa (Carroll et al. 2007, Skelly et al. 2007, Hendry et al. 2008).

When we consider the biological effects of climate change we adopt a time-dimension perspective, in effect moving the three-dimensional spatial worlds of the past and present through the fourth dimension of time. It is also important to keep in mind the variation in the three dimensional world of the present: biodiversity variation (e.g., geographic partitioning of variation such as subspecies) will be retained only if it can thread the needle of present-to-future condition changes. We will have a difficult time predicting what particular aspect(s) of extant variation will be able to thread that needle, although the variation itself might inform us in two ways: Present species distributions often include natural, trans-climatic experiments (e.g., in latitude, elevation, precipitation, temperature, etc.), and extant variation (e.g., in the genome) can be used to understand how these lineages responded to past climates and events. Evaluation of adaptive evolutionary potential within lineages and the application of this information to management is a rapidly growing area (e.g., Chevin et al. 2010, Hoffmann and Sgró 2011).

The diversity of approaches to defining, monitoring, and studying within-lineage microevolutionary changes is also increasing rapidly, and adopting an approach requires careful consideration. Two examples of potential pitfalls might help clarify this, one each from phenotypic

and genotypic perspectives.

In terms of phenotypes, Tellería et al. (2013) advocated standardized measuring in annual banding programs to monitor morphological changes in living birds. We do have much to learn from measuring and banding birds, but monitoring long-term change in such a framework is highly problematic given inter-observer variation (i.e., high measurement error), the low likelihood of having sufficient standards and standardization across decades, and no assurance that the same population is being monitored (see below). They also neglected to mention that measurements from living birds cannot be compared directly to measurements from museum specimens because the latter shrink when prepared and dried (Winker 1993, 1996). We expect changes in the size and shape of characters between living (or freshly dead) birds and museum specimens. This is why the majority of studies that examine morphological changes in wild populations through time involve museum specimens and single observers; the data are better. Also, with museum specimens we have a lot more to work with, enabling genetic, stable isotope, contaminant, and other studies to be conducted as well, both now and into the future.

For a genotypic example, Funk et al. (2012) advocated using genomic data to delineate conservation units by combining the different information that neutral versus adaptive loci provide. Their approach is likely oversimplified, however, especially because the search for adaptive loci is subject to false positives, false negatives, and variation in effective population size (Hughes 2007, Rockman 2012, Bank et al. 2014, Wood et al. 2014). Nevertheless, this field is in its infancy, and genomics holds much promise for management and conservation (McMahon et al. 2014).

Are we working with the same population?

Ranges shift and lineages change over time. Are the populations we focus on today the same

ones that were there historically? This question has two elements. The first is outright human error. In museums, documentation of organisms through specimen preservation has been important in revealing identification errors. Misidentifying species can be a comparatively easy matter to sort out, provided adequate documentation exists, and specimens remain the gold standard. For example, Phillips (1975) used specimens to show that professional and amateur ornithologists alike had for decades misidentified Western Sandpipers (*Calidris mauri*) as Semipalmated Sandpipers (*C. pusilla*) during the nonbreeding season up and down the eastern seaboard of the United States, a region whose avifauna is probably one of the best-known in the world. In contrast, because no specimens were preserved we are not certain about historical changes in eider species on St. Matthew Island in the Bering Sea (Winker et al. 2002).

The second, more difficult element of the problem is when species identification is correct, but changes occur within that species at a particular geographic location. As time series of museum specimens have accumulated, we have become more aware of this issue. Phenotypic changes are being documented in many taxa around the world when historical material is available for comparison (e.g., Pergams and Lawler 2009, Yom-Tov and Geffen 2011). Genetic changes are less frequently sought (costs tend to be higher and there is less material of good quality), but these are also being found (Glenn et al. 1999, Groombridge et al. 2000, Pergams and Lawler 2009, Bourke et al. 2010). Here, too, the existence of preserved material is often crucial, and specimens from today are also important to document the present for future studies of change. Great advances are also being made in measuring phenotype (e.g., Houle 2010, Köhl and Burghardt 2013), and phenotypic changes in one species can have profound effects on local ecologies (Palkovacs et al. 2011).

Entangled populations.—Another important aspect of tracking lineages is recognizing that they often become physically entangled (from a human perspective) with other lineages. For example, the

population being monitored may move or go extinct, it may be replaced by a different population, or it may exhibit relatively rapid changes within the population lineage—all while identifications at the species level show the same species present at a location. Except for the longer-term phenomena of extinction and evolutionary changes within a lineage, in tropical and subtropical locations (especially) physical interpopulation mixing can occur frequently within the annual cycle, causing complex short-term entanglements. And of course migratory populations that are separate (allopatric) while breeding often come together during migration and in winter. Traditionally, subspecies were used to sort out such comingling (e.g., AOU 1957), and these can still be useful (Ramos 1988, Gates et al. 2013), but new techniques are also being applied (Webster et al. 2002). The point is that a simple population census may be misleading, and mark-recapture may fail if dispersal is high (Van Horne 1983, Winker et al. 1995). Counting is susceptible to failure, as is mark-recapture. All of these considerations suggest that monitoring programs should include a specimen archiving component.

An increasingly interdisciplinary approach: retrospective studies

Preserved museum specimens have been critical tools for systematics and taxonomy. But the importance of these disciplines to monitoring change has expanded dramatically as these specimens have accumulated over time and have proven useful for answering questions in other disciplines. It is in this interdisciplinary arena where the specimen-based fields of systematics and taxonomy are likely to have the most impact on big societal questions. A growing interdisciplinary chorus is pointing to the importance of ongoing sampling. Archiving specimens in monitoring programs would thus complement needs in other disciplines, and there are clear synergies appearing. The collections community itself is seeking to rejuvenate collections for traditional, biodiversity research (Wheeler et al. 2011); there are calls to revitalize efforts in natural history (Tewksbury et al. 2014);

and there are also calls from climate change researchers to maintain and extend specimen time series in partnership with global change biologists (Lister et al. 2011, Johnson et al. 2011, Gardner et al. 2014). These broad calls for adding to time series of specimens occur because the benefits of doing so extend well beyond the more traditional specimen-based disciplines of systematics and taxonomy (Suarez and Tsutsui 2004, Winker 2004, IWGSC 2009, Pyke and Ehrlich 2010, Lister et al. 2011, Johnson et al. 2011, Lavoie 2013). These nontraditional uses have little relationship to the research on which collections have historically been based, but they are often tremendously important. These broader uses of collections have been exploding in recent years. Of the 382 nontraditional studies examined by Lavoie (2013), most were published in the preceding 10 years. Some examples of this nontraditional collections research applicable to birds are:

Contaminants.—An early example was research using old egg specimens showing that DDT was having disastrous effects on avian reproduction (Ratcliffe 1967, Hickey and Anderson 1968), resulting in legislation benefitting health on an ecosystem scale (Grier 1982). Museum specimens enabled demonstration of increased mutations following the Chernobyl nuclear accident (Ellegren et al. 1997). Old seabird specimens have been used to document rises in mercury levels in the Atlantic Ocean and high-latitude New World birds (Thompson et al. 1998, Evers et al. 2014).

Population changes/Conservation.—Historical specimens are being used to demonstrate increased levels of environmental stress and morphological and genetic changes through time among extant populations (e.g., Glenn et al. 1999, Groombridge et al. 2000, Lens et al. 2002, Pergams and Lawler 2009, Gardner et al. 2014). Invasive species have also become important in collections-based research (Lavoie 2013).

Environmental and climatic changes.—Collections have also helped reveal long-term, ecosystem-scale changes in the North Pacific Ocean, one of the world's most important fishing grounds (Schell

2000, Hobson et al. 2004). Other studies of stable isotope changes through time in specimen tissues have shown the nature and extent of anthropogenic environmental changes (e.g., Becker and Beissinger 2006, Newsome et al. 2010).

Ecological niche modeling.—Understanding how populations are responding to climate change has been aided by using specimens to quantify the climatic niches that populations and species occupy, and often researchers add resurvey data to enable contrasts through time (e.g., Moritz et al. 2008, Tingley et al. 2009).

In sum, museum specimens have proven to be highly effective (and in many cases crucial) to monitor and measure changes in populations, species, and the environment. Such measures have profound implications for humans and managed biota, and three critical points are apparent: time series are frequently essential (for retrospective studies), today is the past of tomorrow, and the Earth is currently undergoing profound environmental and climatic changes. Museum biologists tend not to do the types of nontraditional collections research that are proving to be so valuable to society, leaving largely to chance the accumulation of adequate samples from today for these nontraditional studies. Museum scientists, biodiversity managers, natural historians, and biologists studying contaminants, conservation, global change, and disease need to work together to change this situation so that society continues to reap these important and diverse benefits.

It is not just complementarity with other goals that is important, however. We are likely to need both genotype and phenotype to understand changes through time in the populations we monitor. For example, Karell et al. (2011) found rapid morphological change associated with climate change in the Tawny Owl (*Strix aluco*), and Stuart et al. (2014) found that phenotypic changes in island populations of *Anolis* lizards occurred following just 20 generations after the introduction of a congeneric competitor. In both cases, long-term studies on these populations enabled us to know

these changes were occurring in the same population lineages through time instead of being population replacement through dispersal or supplanting. Intense long-term study (e.g., with individual marking) is expensive and not warranted for most monitoring studies. Archiving some specimens is an economical way to overcome this issue. It is also a way to lay in samples that allow us to retrospectively monitor lineages that we didn't even know we should be monitoring in the past. Today, diverse research questions about changes in birds are using these resources to study topics such as migratory connectivity (Hobson et al. 2010), hybrid zone dynamics (Curry and Patten 2014), and population demography (Spurgin et al. 2014). There is enormous bang-for-buck in a preserved bird specimen, not least because as new advances in methods and new questions emerge you can go back to a specimen to look for things we didn't even know to look for at the time the specimen was preserved. In the future, science will be better than it is today, and we can contribute directly to that improvement by providing quality data and samples from the present.

Systematics at community and assemblage scales

Systematics and taxonomy intersect with conservation, management, and monitoring from an among-lineage perspective, too. Incorporating phylogenetic relationships into ecosystem management is as or more important than focusing management or monitoring on a single lineage. In conserving biodiversity, all lineages are not equal when we consider that we should preserve evolutionary history as well. Who can predict which lineages will ultimately be successful? As a simple example, preserving six species in one genus is an evolutionarily poorer achievement than preserving six species in six genera; the latter preserves more phylogenetic or evolutionary distinctness. We can effectively couple advances in evolutionary biology with conservation and management to enhance outcomes. As we increasingly work to manage ecosystems, these

approaches, though complex, are becoming more important (Vane-Wright et al. 1991, Nee and May 1997, Isaac et al. 2007, Diniz-Filjo et al. 2013, Forest et al. 2015).

Going forward

Taxonomically, we will see an increasing number of bird species recognized and a decreasing number of traditional subspecies—some will be raised to full species and others will be eliminated as representing clinal variation. These changes will happen not because of changing species concepts, but rather as a consequence of more data and an improved understanding of avian diversity and its distribution. Del Hoyo and Collar (2014) summarized 30 species lumped and 462 split as full species in the world's non-passerines (though not all these splits are acceptable; Remsen 2015). Fjeldså (2013) estimated that when avian diversity has been fully evaluated there will be about 12,000 species. This is an increase of about 20% over what we thought existed a few decades ago. Our understanding of relationships among these taxa also continues to change (Jarvis et al. 2014).

Although molecular genomics will provide a great deal of useful information, particularly about historical attributes of populations, much of the signal in the data is neutral variation, and its geographic distribution may or may not indicate phenomena of evolutionary importance. Phenotype, on the other hand, should be assumed to be adaptive (as a null hypothesis), particularly when it is distributed heterogeneously across a species' range. Integration of both types of data will increase.

In monitoring change, quality of historical data will always be an issue, and today is tomorrow's past. Thus, it is important that we archive quality data from the present. We can also see that the potential for archived specimens is much greater than initially realized, yet museum collections are not yet being adequately developed to meet important interdisciplinary needs. Fortunately, as interdisciplinary impacts become more widely appreciated and ornithologists

continue to expand their toolboxes, we are likely to see a rapid increase in use of the tools of systematics, taxonomy, and population genetics for monitoring avifaunal change.

Glossary

Coalescent methods: analyses of DNA data based on coalescent theory, in which gene genealogies are reconstructed in a retrospective manner focusing on the most recent common ancestor(s) of current alleles or haplotypes. Models are run using various assumptions to determine which best fit the data. These methods are often used to estimate time to most recent common ancestor, effective population size, and gene flow.

Diagnosable: sufficiently distinct to be identified as belonging to one group rather than another. Often used in systematics in a cladistic, either/or, or present/absent manner. In population genetics and taxonomy, particularly at the subspecies level, we use probabilities instead, and thresholds of diagnosability are usually used (e.g., the 75% rule for subspecies; Patten 2010).

Effective population size (N_e): the number of individuals in a population that successfully reproduce, which is almost always smaller than the census size (long-term effective population size can be higher in populations that have experienced severe declines).

Evolutionarily significant unit: a population that is different and separate from other populations, as determined using phenotypic or neutral genetic characters.

Gene flow: the movement of genes from one population or lineage into another.

Genetic drift: the change in allele frequencies in a population through random sampling of individuals (through survival) and their alleles (through reproduction). Genetic variation is often lost through this process, decreasing that variation (if the rate exceeds that of mutation) and leading to lineage sorting between populations and species.

Lineage: a group of organisms united by common descent, whether at population, subspecies, species, or higher taxonomic level.

Population genetics: the study of genetic variation and related evolutionary processes within and among populations; genome-scale datasets seem poised to transform this field into population genomics.

Selective sweep: occurs when an allele that is selectively advantageous undergoes such strong positive selection that it sweeps to dominance or fixation, dramatically lowering or even eliminating genomic variation at that locus (and nearby sequence) in a population. In the nuclear genome, the signal of a selective sweep is broken up over time through recombination.

Species delimitation: determining species limits and thus discovering species-level biodiversity.

Systematics: the study of organismal diversity and phylogenetic relationships.

Taxonomy: the theory and practice of describing, naming, and classifying organisms.

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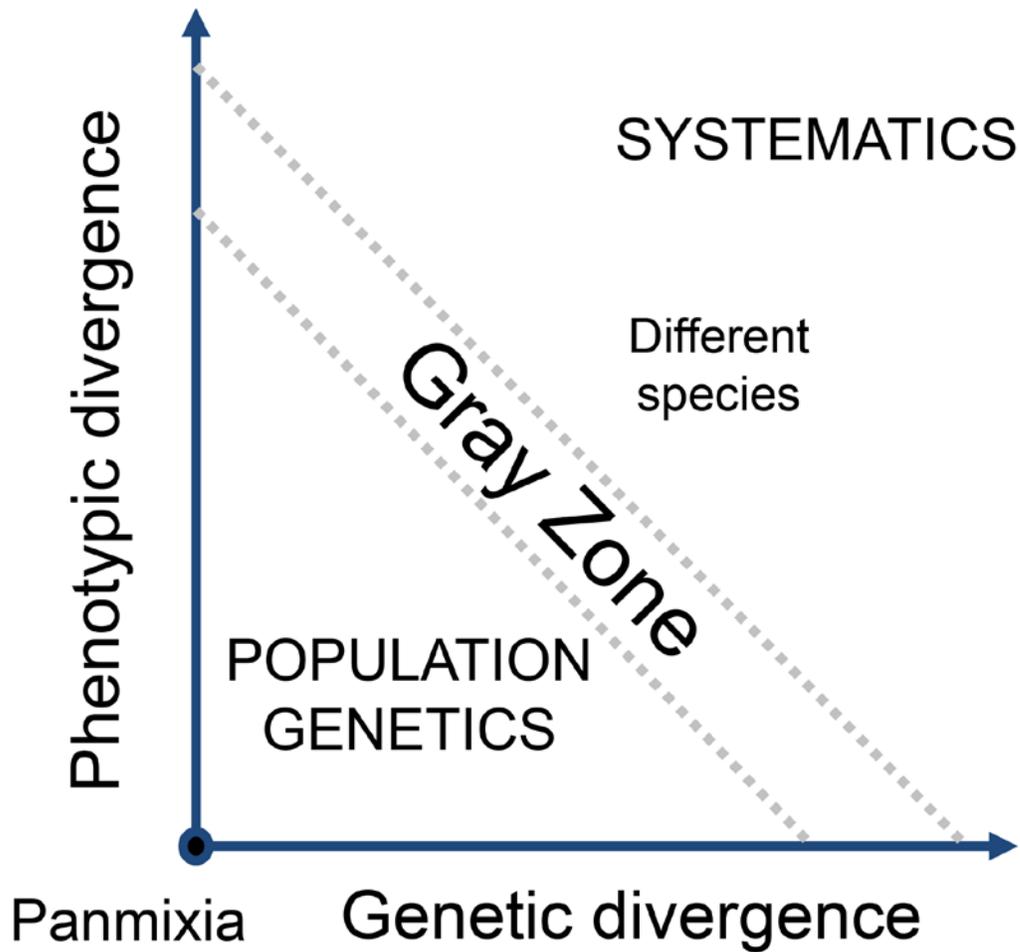


Figure 1. Evolutionary divergence depicted for heuristic purposes as a simple, two-dimensional process space. The two main axes of divergence, phenotype and genotype, represent largely adaptive and largely neutral attributes, respectively, in the major data sets used to describe and study biodiversity (adapted from Moritz 2002). Differentiating pairs of units (populations, subspecies, etc.) progress from panmixia (complete genetic admixture) to and past speciation in this space. The gray zone reflects uncertainty in species delimitation and the variation among species concepts in exactly what constitutes a species. The fields of population genetics and systematics dominate different areas of this process space.

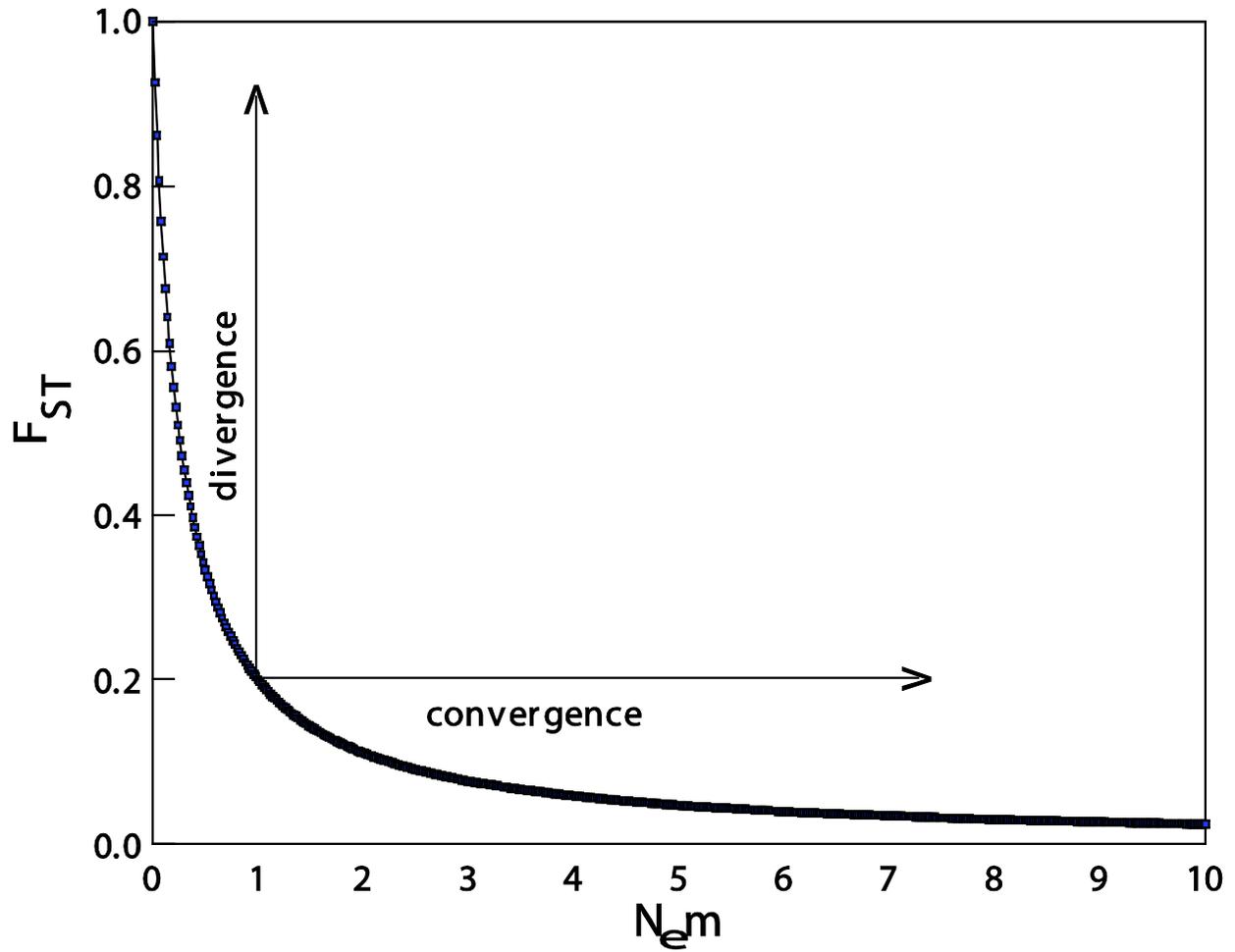


Figure 2. The relationship between population differentiation (Wright's 1943 F_{ST}), and the product of effective population size (N_e) and the rate of gene flow (migration, or rate of effective gene flow), m . Not only is the relationship highly nonlinear, but the inflection point, at which populations switch from diverging to converging, occurs at just one migrant per generation ($N_e m = 1.0$), under neutral conditions (after Cabe and Alstad 1994).