

Chapter 2

Integrative Taxonomy of Birds: The Nature and Delimitation of Species



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Abstract Species are the basic currency in biodiversity studies, but what constitutes a species has long been controversial. Since the late 1990s, debates over species have shifted from theoretical questions (e.g., What is a species? Which species concept is best?) to empirical questions (How can we document species both efficiently and accurately?). A growing number of taxonomists agree that species can be discovered and documented in many different ways, preferably by employing and combining multiple types of evidence (“integrative taxonomy”). This chapter examines how and why avian taxonomy has become integrative, how species hypotheses are documented and falsified, and how the growth of taxonomic knowledge provides new and valuable insights into the speciation process, biogeography, and conservation biology.

Keywords Aves · Integrative taxonomy · Pluralism · Speciation · Species criteria · Species limits

2.1 The Centrality of Species

The concept of species is one of several key concepts in biology (Keller and Lloyd 1992; Pigliucci and Kaplan 2006; Sober 2006). While the discovery, description, and naming of species are strictly the responsibility of taxonomists, species are important in many other disciplines in society, including conservation (IUCN list of endangered species), health care (e.g., infectious diseases), and law (CITES, ESA; Geist 1992). Species are crucial for various concepts in other branches of biology, and society in general, as reflected by such terms as “keystone species” (ecology), “flagship species” (conservation), “speciation” (evolutionary biology), and “speciesism” (ethics). In biology the concept of species is shared across various hierarchies

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Table 2.1 Species are important in and shared among various hierarchies

Ecology	Taxonomy ^a	Genealogy	Conservation
	Domain		
	Kingdom		
Ecosphere	Phylum		
Biome	Class		
Regional ecosystem	Order		Landscape
Local ecosystem	Family	Tree of life	Ecosystem (service)
Community	Genus	Monophyletic group	Habitat
Species	Species	Species	Species
Population	Subspecies	Deme	ESU
Organism		Organism	Management unit
Organ system		Genome (germ line)	Population/breed
Organ		Gene	Genetic diversity
Tissue			Adaptation
Cell			Gene

^aSee Dubois (2006) for a much more extensive set of categories

(Table 2.1). The broad relevance of species does not mean that the term species means the same thing to different biologists or that species taxa are uniform across groups. Far from it.

2.2 Why Is There a Species Problem?

There are numerous reasons why many professional biologists and philosophers have different opinions about “species.” It is impossible to do justice to this rich debate in only a few paragraphs, so I will only briefly discuss the main points of contention. For the purpose of showing the diversity of opinion, I contrast the most divergent views, but it should be noted that there are numerous intermediate viewpoints.

2.2.1 *Monism vs. Pluralism*

A major issue among philosophers of science and more philosophically inclined systematists is the question whether species possess a single, unique quality that differentiates them from all other categories. Pluralists believe that there is no single unified way to delimit species; nature can be viewed from a multitude of perspectives which are equally valid. Most philosophers of science seem to agree that this is extremely likely and that pluralism is the only realistic approach. There are at least two brands of pluralism. One suggests that there are many permissible ways to classify

species in any given situation, depending on the needs of the particular biologist (Kitcher 1984). Thus, ecologically defined species of ducks are just as acceptable as phylogenetically or morphologically defined species of ducks. The other suggests that in each group there is only one optimal classification, but that the optimal criteria to classify species may differ among groups (Mishler and Donoghue 1982).

The opposite view is monism, which holds that there is a single optimal way to divide nature into species. This is the view preferred by most biologists, because they would like to find *the* answer to the species problem and preferably have this derived from first principles in evolutionary biology or systematics (Ruse 1969; Pigliucci and Kaplan 2006).

2.2.2 *Realism vs. Anti-realism*

The issue of whether there is one or more than one valid way to classify species is closely related to the question of whether species taxa are real. Not surprisingly, monists (i.e., most biologists) tend to accept that species exist independent of our ability to recognize or find them. For instance, Mayr (1982) noted that variation is often discontinuous and that nature consists mostly of discrete units. Diamond (1966) demonstrated that members of “primitive” human tribes in New Guinea classify local birds in almost exactly the same way as professional taxonomists. Modern taxonomists may further point out that in many cases, different taxonomic methods identify the same species units, indicating that such species are not a fabric of the human mind.

Opponents of this view are not convinced by such observations and have argued that discrete groups are sometimes elusive, that all species are connected vertically through their ancestry, or that there is simply nothing special about species. The view that species are not real, i.e., that they have no objective reality outside of the human mind, is also called “nominalism” (Stamos 2003). Modern-day adherents to this view typically come from a background in either botany (where species limits tend to be more blurred by gene flow than in zoology) or paleontology (where inferring species limits through time has always been considered difficult). Botanist Van Valen (1976), for instance, noted that the classification of oaks is so problematic as a result of gene flow that it is impossible to find any discrete species. He asked “why can’t there be taxa without species?” In his presidential address to the Paleontological Society, Shaw (1969) argued that species are not real (and should be abandoned), because drawing species limits in time is completely arbitrary. Mishler (1999) emphasized that all taxonomic ranks are arbitrary, but that clades are real. He argued that in a truly phylogenetic system, there is no place for ranks and as a consequence, no place for species. In his view, species are phylogenetic groups just like higher taxa, and all other putative properties of the species rank that have been proposed by various taxonomists (phenetic groupings, interbreeding, reticulation) can also be found at other ranks or are inconsistent with phylogenetic groups.

2.2.3 *Theoretical vs. Operational*

Philosophers of science have proposed several theoretical “solutions” to the species problem. These include the idea that “species are individuals” (Ghiselin 1974) or that “species are relations” (Stamos 2003). However, these do not connect with taxonomic practice. The Hennigian species concept, which proposes that species can be delimited in time by branching events (nodes) and extinction events (Hennig 1966), has also been proposed as a solution (Ridley 1989) but fails for the same reason. A formal description of this species concept (Kornet 1993) is mathematically sound, is universally applicable, and is able to assign every individual organism to a species. Yet, this method is hopelessly unrealistic because one needs to know the position of every individual within the genealogy.

At the other end of the spectrum is the phenetic school, which is completely theory-free (Sokal and Crovello 1970). However, without any theoretical underpinnings, it is impossible to determine which of many methods to group individuals into “species” is the best. The phylogenetic species concept defines species as “the smallest diagnosable cluster of individual organisms within which there is a parental pattern of ancestry and descent” (Cracraft 1983) but does not tell what those species are beyond the somewhat vague “evolutionary units.”

It is safe to say that theoretical concepts are usually not very strong operationally and that operational concepts do not tend to be strong theoretically (Hull 1997, 1999). Both aspects are connected, because in order to know how one should find species, one must first know what to look for. Whereas many biologists would agree with Cracraft (2000) that a species concept “should work,” no species concept is entirely satisfactory without a solid theoretical basis.

2.2.4 *Pattern vs. Process*

Some species concepts emphasize evolutionary mechanisms and processes, such as mate choice, species recognition, interbreeding, hybridization, and gene flow, whereas others focus on the results and patterns of evolution (such as diagnosability, monophyly, and congruency). The biological and recognition concepts are examples of process-based species concepts, whereas phylogenetic, monophyletic, and inter-nodal concepts are pattern-based approaches. Evolutionary biologists and population geneticists tend to prefer process-based species concepts, whereas taxonomists and phylogeneticists tend to prefer pattern-based approaches.

2.2.5 *Prospective vs. Historical*

Under the biological species concept, taxa are recognized as species, if they remain “reproductively isolated,” in the sense that they do not fuse into a single population (Mayr 1982, 1996). The BSC, therefore, is prospective (O’Hara 1993, 1994; Maddison 1997); only future events will show whether currently recognized taxa remain reproductively isolated or fuse into each other.

The alternative viewpoint is that species-level taxa should be delimited on the basis of historical subdivisions (i.e., historical patterns), rather than present-day or possible future interactions and processes (Lidén and Oxelman 1989), such as hybridization and gene flow. Maddison (1997) argued that species concepts which are prospective and which require speculations about the future are not helpful in biology; since all of our data are of the present and past, the units by which we interpret these data must also be strictly historical. There are two major kinds of historical units: species as clades and species as lineages. The species-as-clades view was developed by Donoghue (1985) and de Queiroz and Donoghue (1988, 1990) and considers phylogenetic species to be the smallest *monophyletic* groups of organisms supported by autapomorphies (unique derived character states). The species-as-lineages view regards species as (parts of) branches in a phylogeny (Mayden 1997; de Queiroz 1998, 1999).

2.2.6 *Concerns by End Users*

Some end users of species have been very vocal about how taxonomists should delimit species. For instance, some conservationists and biodiversity scientists have complained that if pattern-based species concepts were to be implemented widely, the number of species would become “too high” (e.g., Agapow et al. 2004) and result in “pseudoreplication” of species (Isaac et al. 2004). Other complaints made by some end users of taxonomy are (1) that taxonomists have recognized species on the basis of “trivial” morphological character differences or molecular differences (Collar 1997; Tobias et al. 2010), (2) that taxonomy has become “unstable” due to the use of phylogenetic species concepts (Isaac et al. 2004; Mace 2004), and (3) that species designations no longer correspond to genetically incompatible populations (affecting captive breeding and reintroductions; Frankham et al. 2012). These are not scientific (i.e., empirical) concerns, but they do illustrate what some end users have come to expect from species.

All these viewpoints underscore the many dimensions of the species problem. An important insight was that the species problem actually comprises several distinct problems (e.g., Frost and Kluge 1994; Reydon 2004): What are species? How do species originate? How can, may, or should one delimit species in practice? It seems obvious that one should have a good sense of what species are before one can tell

how species originate or how to delimit species. Thus, the concept of species is the primary problem. This set the stage for a major breakthrough in the late 1990s.

2.3 The Lineage Concept

The lineage concept of species was first articulated by Simpson (1951) and further developed by Hennig (1966), Wiley (1978), and Wilson (1995). These authors viewed species as branches in the tree of life. This view was long known as the “evolutionary species concept” or “Hennigian species concept.” Because these views were not accompanied by, and did not easily translate into, operational criteria, these have long been ignored by taxonomists (but see Frost and Hillis 1990). The idea that species are best seen as lineages gained strong support in the late 1990s due to three now-classic publications by Richard Mayden and Kevin de Queiroz (Mayden 1997; de Queiroz 1998, 1999). Their case rested on two important insights.

First, there is a fundamental distinction between the *species concept* (primary species concept, Mayden 1997), which tells us what species are, and *species criteria* (secondary species concepts, Mayden 1997), which describe how species taxa may be delimited in practice. Both Mayden and de Queiroz observed that most species concepts are actually little more than prescriptions of how species should be delimited (i.e., species criteria). Thus, many “species concepts” have confounded operational and theoretical aspects of species and have defined the items to be discovered by the discovery process (Frost and Kluge 1994).

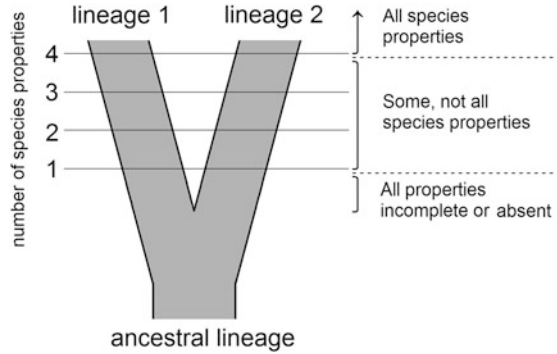
Second, most views on species and species criteria are consistent with the idea that *species are segments of population lineages* (de Queiroz 1998, 1999), i.e., branches or parts of branches in the tree of life. Although some criteria can only be applied at one time-slice (e.g., reproductive isolation), it does not follow that species are only real at that point in time, and this does not preclude one from seeing such species as lineages.

2.4 Corollaries of the Lineage Concept

The lineage concept does not by itself dictate how species should be delimited, but it provides a few important hints. First, because different species may have different properties, all traditional species criteria are potentially relevant for finding species. Importantly, different species criteria highlight different aspects of species. Thus, it makes sense to apply as many criteria as possible, not only to avoid overlooking species but also to describe and better understand the nature of these species taxa (Sangster 2014).

Second, there is no reason to presume that all the properties identified by traditional species concepts evolve in all lineages, let alone all at the same time. Thus, a species may exist even if it does not possess one’s preferred species criterion

Fig. 2.1 Different species properties (e.g., reproductive isolation, diagnosability, monophyly, ecological niches) may evolve at different times during divergence. The absence of a particular property (e.g., property 4) does not falsify species rank, if there is other evidence that it is a separate lineage (e.g., properties 1–3)



(Fig. 2.1). The absence of a particular species property does not mean that the lineage itself does not exist. This is an important observation, because from this it follows that *no property can be considered “defining” for species* (de Queiroz 1999, 2007). This explicitly rejects the equality of species; some may possess all properties, others may not; some may be highly distinctive, others are cryptic; some may be monophyletic in a gene tree, whereas others are not; some may be reproductively isolated, but others may not.

Third, if species are lineages, then the species delimited by taxonomists are *hypotheses of lineages*. Thus, species are not simply described (“facts”), but their existence is a testable hypothesis. Like any other scientific statement, these should be documented as thoroughly as possible.

2.5 Integrative Taxonomy

Integrative taxonomy may be considered the operational counterpart of the lineage concept. The term “integrative taxonomy” was introduced almost simultaneously in two papers which appeared in 2005 (Dayrat 2005; Will et al. 2005). Both papers emphasized that it is important to combine and integrate multiple approaches to species delimitation. Will et al.’s (2005) motivation for their paper was to provide a critique of barcoding, which is the use of a single line of molecular evidence to identify and discover species. Ironically, it later became apparent that barcoding may also be a valid part of integrative taxonomy, because it may produce new hypotheses of species taxa, which may be tested, refined, falsified, or corroborated by other evidence (Padial and de la Riva 2007).

2.5.1 *Why Multiple Data?*

Seeking multiple lines of evidence to document species taxa is a logical consequence of the view that species taxa are hypotheses. Indeed, it is common sense that a hypothesis is better confirmed by different kinds of evidence than by more evidence of the same kind. It also can be rationalized from Bayesian principles. Each time a hypothesis is confirmed by the same kind of evidence (e.g., morphology), the probability expressing the degree of belief that it will do so in the future gradually increases. On the other hand, the prior probability that a hypothesis is confirmed by another type of evidence (e.g., reproductive isolation) may initially be quite low. Therefore, finding that the hypothesis is confirmed by a new line of evidence represents a significant increase in the probability that the hypothesis is true (Chalmers 1999). The validity of questionable species taxa based on small numbers of specimens or small numbers of characters is often addressed with other datasets, typically molecular data (e.g., Bensch and Pearson 2002; Sangster et al. 2016a; Pérez-Emán et al. 2018). Another reason why it is best to seek multiple kinds of evidence is that all taxonomic criteria have both strengths and weaknesses (Table 2.2).

2.5.2 *Why Integrate?*

Although the use of multiple lines of evidence in taxonomy is not new, the emphasis on integration of evidence is novel. Collecting multiple kinds of evidence is not enough, for several reasons. As noted above, various species criteria are complementary, because these highlight different aspects of lineage divergence. Sometimes the interpretation of one type of evidence depends on information on other properties. For instance, to demonstrate that two putative sympatric species are reproductively isolated, it is often necessary to demonstrate that these species are diagnosable or reciprocally monophyletic. Evidence for species may be scattered across various papers and thus should be collected and assessed together. Thus, integrative taxonomy may be defined as *the theory and practice of documenting and evaluating hypotheses about the taxonomic status of putative species by integrating multiple lines of evidence.*

2.6 Strengths of Integrative Taxonomy

By combining and integrating taxonomic evidence in a single approach, integrative taxonomy has several qualities that distinguish it from traditional approaches.

First, if one views different kinds of taxonomic data as complementary accounts of species divergence, it becomes apparent that many taxonomic conflicts are not based on incompatible interpretations of species limits but simply stem from

Table 2.2 Strengths and drawbacks of various species criteria

Criterion	Strengths	Drawbacks
Diagnosability (fixed difference in heritable character)	Easy to apply Cost-effective Applicable to a broad range of taxa Applicable to a broad range of data types Can be expressed in statistical terms (e.g., Wiens and Servedio 2000)	Heritability often unknown Sample size dependent Nonheritable differences may also identify evolutionary units (e.g., song, biometric differences) Difficult to apply to sequence data
Degree of difference (phenotypic/genetic divergence)	Phenotypic divergence: appeals to the wish for “good species,” popular among end-users of taxonomy Genetic divergence: easily obtained as by-product of phylogenetic analysis	Requires a better supported reference taxonomy (Sangster 2000) Cutoff point typically arbitrary Difficult to apply in complex taxonomic problems May conflict with phylogenetic relationships
Reproductive isolation (intrinsic barriers to gene flow)	Often point of no return (permanent lineage divergence) Mechanism of maintenance of species boundaries	Limited scope: cannot be applied directly in allopatry, at different time slices, or in paleontology Requires prediction of future interactions Ability to interbreed is plesiomorphic: reproductive compatibility may conflict with phylogenetic relationships Arbitrary: many species hybridize; when are species (not) reproductively isolated? Degree of gene flow/isolation may differ among genes
Prezygotic isolation	Biological meaning (“species recognition”)	Recognition or cues may be dependent on environment, phase of breeding season Density dependence: degree of interbreeding may depend on the availability of homospecific partners (Hubbs’ rule)
Postzygotic isolation	Biological meaning (“genetic incompatibility”)	Extremely hard to document Application beyond expertise of most trained taxonomists Fitness of hybrids and/or parental species may vary with local circumstances (e.g., bounded hybrid superiority; Moore 1977)
Non-monophyly	Removes nonhistorical units	Only a suitable basis for splitting if two taxa are not sisters (other evidence is required if the two “species” are nested)

(continued)

Table 2.2 (continued)

Criterion	Strengths	Drawbacks
Reciprocal monophyly (of gene trees)	Demonstration of historical isolation Easy to apply	Cannot be used in isolation (monophyletic groups exist at many levels, so further evidence is required) Evolves slowly, thus prone to type II errors Choice of loci is arbitrary Monophyly may be based on chance, rather than historical isolation (Irwin 2002)

differences in the sensitivity of taxonomic criteria. For instance, the finding that two diagnosable species do not form reciprocally monophyletic groups does not represent a major taxonomic dilemma but is best interpreted as a case where one property (diagnosability of morphological character states) simply became fixed before the other (exclusive coalescence of gene trees). Thus, integrative taxonomy may lay numerous taxonomic controversies to rest.

Second, integrative taxonomy is an efficient approach to taxonomy. Because evidence for species rank is not limited to one (“defining”) property, integrative taxonomy may be informed by all kinds of available data.

Third, the integration of different kinds of evidence may help to discover additional species. Evidence which is not very relevant or informative in isolation may be crucial when combined with other evidence. For instance, the finding that two migratory subspecies of Bean Goose *Anser fabalis* have overlapping wintering ranges in Western Europe is not remarkable nor is their return to different breeding areas in Siberia (Burgers et al. 1991). However, when combined with the knowledge that high-latitude species of waterfowl find their mates on the wintering grounds, these findings become very significant for taxonomy. If pair formation takes place on the wintering grounds, then both forms have the opportunity to form mixed pairs. If no birds ringed in winter return in the breeding area of the other form, then this is prima facie evidence that the two are not forming mixed pairs and remain reproductively isolated (Sangster and Oreel 1996). This hypothesis received some further support from the findings that both groups formed separate groups in a molecular phylogeographic analysis (Ruokonen et al. 2008) and may not even be each other’s closest relatives (Ottenburghs et al. 2016).

Fourth, examples such as these highlight the fundamentally analytic and iterative nature of integrative taxonomy and underscore that species delimitation is a science (Yeates et al. 2011; Sluys 2013). Thus, modern taxonomy is more than a mere baptismal act or a one-time “description.” Hypotheses of species rank require documentation and reassessment in the light of new evidence, just like any other scientific hypothesis.

Finally, by including all species criteria under a single unified approach, integrative taxonomy shifts away attention from the yes-or-no question of whether or not

Table 2.3 Examples of falsifications of species limits based on defining criteria

Species pair	Original hypothesis of species distinctiveness based on:	Proposed falsification of species status based on:
Ducks: <i>Anas carolinensis</i> — <i>A. crecca</i>	Non-sister group relationship (paraphyly with respect to <i>A. flavirostris</i>) High level of sequence divergence (mtDNA) Diagnostic differences in male plumage (Sangster et al. 2001)	Inferred gene flow of nuclear DNA (Peters et al. 2012)
Giant petrels: <i>Macronectes halli</i> — <i>M. giganteus</i>	Sympatric (allochronic) breeding Plumage and bare parts (diagnostic differences; Bourne and Warham 1966)	Low genetic divergence (<1%; Penhallurick and Wink 2004)
Kites: <i>Milvus fasciicauda</i> — <i>M. milvus</i>	Plumage (diagnostic differences; Hazevoet 1995)	Non-monophyly of cytochrome b sequences (Johnson et al. 2005)
Owls: <i>Otus madagascariensis</i> — <i>O. rutilus</i>	Plumage and vocalizations (diagnostic differences, Rasmussen et al. 2000)	Non-monophyly of ND2 sequences (Fuchs et al. 2007)

species A meets the criterion of species concept X but instead focuses on the information content of the total body of evidence.

2.7 What Is Not Integrative Taxonomy?

Many types of data, analyses, and criteria can be valid parts of integrative taxonomy, but this is not to say that anything goes in integrative taxonomy. At least two approaches are inconsistent with integrative taxonomy: (1) the falsification of species rank by invoking a “defining” criterion and (2) the use of a set of “standard” criteria that restricts the scope of taxonomic fact-finding.

2.7.1 Falsification by a “Defining” Species Criterion

Species taxa may show many different combinations of species properties, and not every property may be present in each species (Fig. 2.1). Thus, it is important to keep in mind that *while any particular species property may help to document the existence of a species, its absence in other species does not falsify their species rank* (de Queiroz 2007). From this, it follows that a hypothesis about the validity of a species taxon can only be falsified if all lines of evidence supporting that taxon are falsified. Unfortunately, this is sometimes overlooked. Table 2.3 lists several recent instances where a “defining” criterion was used to falsify species that had been

recognized on the basis of other evidence. In each of these cases, the authors have added new data but have inappropriately placed that evidence above all previous evidence. Some authors have used this strategy to draw far-reaching but highly dubious conclusions. For instance, Johnson et al. (2005) suggested that the Cape Verde Kite *Milvus fasciicauda* “does not exist,” because cytochrome *b* sequences of that species were nested phylogenetically within those of the Red Kite *M. milvus*. This ignores not only that these species are still diagnosable by plumage characters (Hazevoet 1995) but also that non-monophyly may simply result from incomplete lineage sorting due to recent speciation—a common phenomenon in bird species (reviewed by Funk and Omland 2003; McKay and Zink 2010) of which new examples are still being discovered (Päckert et al. 2012; Luna et al. 2017). Appeals to defining criteria will no doubt continue to be made in the taxonomic literature but should be resisted, because it results in unnecessary confusion and instability. This is especially true, if defining criteria differ from paper to paper (as suggested by Table 2.3).

2.7.2 *Standardization of Species Criteria*

A recent proposal attempted to standardize the assessment of species limits by limiting this process to a small number of data classes and a few characters per class (Tobias et al. 2010). This set of criteria explicitly excluded entire data classes that are commonly used in taxonomy (molecular data, phylogenetic data, multivariate analyses, and detailed evidence from hybrid zones). The approach put forward by Tobias et al. (2010) seems to be rooted in what philosophers of science call “anti-realism”: the merit of the criteria is defined in terms of their generality and simplicity, not in terms of whether these result in the delimitation of real evolutionary units. This is underscored by the taxonomic revisions that resulted from application of these criteria (del Hoyo and Collar 2014, 2016), which include several species that modern molecular phylogenetic studies have documented as paraphyletic assemblages of multiple distinct taxa (e.g., Golden-fronted Woodpecker *Melanerpes aurifrons*, Red-crowned Parakeet *Cyanoramphus novaezelandiae*, Mourning Wheatear *Oenanthe lugens*; see Kearvell et al. 2003; Schweizer and Shirihai 2013; García-Trejo et al. 2009; Rawlence et al. 2015). The criteria put forward by Tobias et al. (2010) are inappropriate, because the lineages that we call “species” are things that we discover, not create. Taxonomy is a fact-finding endeavor; any practice that limits, distorts, or interferes with this endeavor should be abandoned.

Attempts to falsify species taxa by appeal to a particular defining criterion and pleas to standardize species taxonomy by limiting its scope can be viewed as attempts to prescribe how species *must* be found, so that any species not found by that method is not a species. The flaws of this approach may be illustrated by analogy to a criminal court case. Taxonomy and the criminal justice process share many similarities owing to the fact that both strongly rely on empirical data (Table 2.4). Like a criminal court case, the task of species taxonomy is to assess objectively what

Table 2.4 Similarities between the empirical aspects of species-level taxonomy (evaluating species limits) and the criminal justice process (evaluating guilt)

Aspect	General principle	Taxonomy (species limits)	Criminal justice (guilt)
Aim	Assess objectively what has happened	Speciation (<i>has speciation occurred?</i>)	Crime (<i>did this suspect commit this crime?</i>)
Hypotheses	The null hypothesis should be accepted unless sufficient evidence shows this to be false	H ₀ : no lineage separation has occurred (taxa must not be recognized as species) H ₁ : speciation has occurred (taxa are best treated as species)	H ₀ : defendant is innocent (and must be acquitted) H ₁ : defendant committed the crime
Strategy	<i>Document</i> the best explanation for the observed evidence; rule out alternatives	(1) Collect as much evidence and as many types of evidence as possible; (2) integrate evidence; (3) define scenarios; (4) evaluate and compare the evidence for all plausible scenarios; repeat, if necessary	Idem
Evidence	Reliance on <i>empirical</i> data	<i>Examples</i> : morphology, genetics, bioacoustics, behavior	<i>Examples</i> : eye witness testimony, DNA fingerprinting, examination of physical objects, written confession
Quality assessment	Assessment of quality (meaning) of the evidence	<i>Examples</i> : rule out misidentification (of specimens), contamination (of DNA samples), inappropriate methodology, effects of small sample size or poor reference data, comparison among non-homological character states	<i>Examples</i> : rule out misidentification (of people or objects), contamination (of DNA samples), inappropriate methodology, effects of small sample size or poor reference data
Complementarity of evidence	Multiple evidence is good; multiple <i>independent</i> lines of evidence is even better	<i>Example</i> : finding a diagnostic bioacoustic character state <i>plus</i> reciprocal monophyly of DNA is more convincing evidence for lineage separation than finding two diagnostic bioacoustic character states	<i>Example</i> : two credible witnesses saying the same thing is good, but a single credible witness <i>plus</i> DNA evidence is even better
Integration of evidence	Different lines of evidence highlight	<i>Example</i> : bioacoustic data may show a pattern	<i>Example</i> : an eye witness may describe what

(continued)

Table 2.4 (continued)

Aspect	General principle	Taxonomy (species limits)	Criminal justice (guilt)
	different aspects; must be <i>integrated</i>	(consistent differences in songs), playback tests may highlight lack of mate recognition, DNA data may show the result (lack of gene flow) (see also Table 2.2)	happened, whereas DNA may tie the defendant to the crime scene
Uniqueness	Each species/criminal court case is unique	No single type of evidence (or combination thereof) can be assumed to “work” in every case	Idem

has happened at some time in the past. In both cases, a hypothesis must be documented, and alternative hypotheses must be excluded. Those who assess and evaluate the hypothesis did not witness the relevant events and thus have to rely on *evidence*. Needless to say, the more evidence the better. Having multiple types of evidence is better than having more of the same type of evidence. If multiple kinds of evidence tell the same story, this increases the plausibility of the hypothesis. Speciation (like a criminal act) may have been a complex, protracted process, and therefore multiple types of evidence may be useful to highlight various aspects of this process. In many cases, these lines of evidence are *complementary* and must be *integrated*. In addition, each pair of species (just like each crime) is unique in one way or another, and there is no a priori reason to suspect that a single type of evidence works in all cases. Finally, like a criminal court case, taxonomy is an *iterative* process. When important new evidence emerges, the original hypothesis must be evaluated again within the light of all available evidence. To argue which species criterion should be adopted as the defining criterion in taxonomy is just as futile as arguing which single type of evidence should be used to “define” guilt in all criminal court cases. Any attempt to a priori limit the evidence used to evaluate a taxonomic case study interferes with the fundamentally empirical nature of taxonomy.

2.8 The Dynamics of Taxonomic Change

After the official start of zoological nomenclature in 1758, the number of bird species recognized by taxonomists increased steadily until reaching a peak in the early twentieth century (Fig. 2.2). During the 1840s, zoologists Carl Sundevall and Herman Schlegel began to treat poorly defined species as geographical races

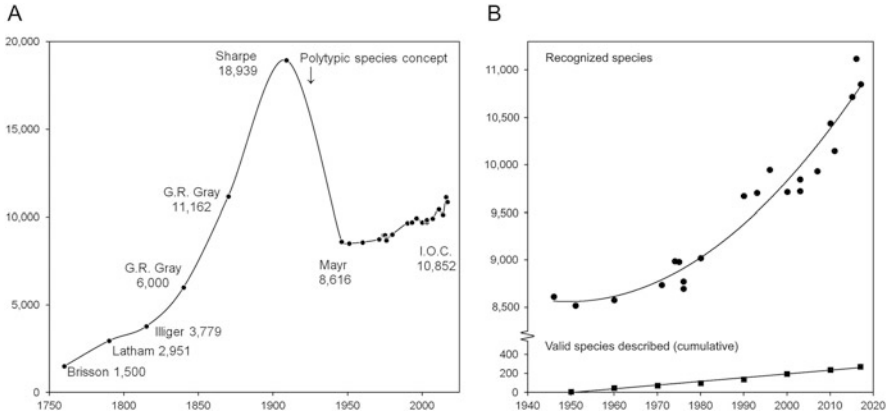


Fig. 2.2 (a) Trends of the total number of recognized species of recent birds from 1760 to 2017. Note the dramatic (>50%) reduction in the number of recognized species between 1909 (Sharpe) and 1946 (Mayr) and the *relatively* slow increase since 1946 (*Updated from Haffer 1992*). (b) Trends of the total number of recognized species of recent birds (upper panel, based on various estimates and classifications, as indicated by the filled circles) and newly described species of birds (lower panel) from 1946 to 2016. Note that the number of recognized species increases much faster (c. 92 species per year in 2007–2017) than the number of newly described valid species (c. 5.3 per year). A second-order trend line was added to illustrate the trend (*Updated from Sangster and Luksenburg 2015*)

(subspecies). In subsequent decades, increased exploration and collection of specimens led to improved understanding of the geographic and morphological continuity of previously recognized species. In the second half of the nineteenth century, a growing number of zoological works started ranking taxa as subspecies (Stejneger 1884). During this period, intergradation became the cornerstone of subspecific taxonomy (Allen 1871). According to this view, subspecies are distinguishable forms that intergrade, whereas species do not intergrade (Stejneger 1884). Because the criterion of intergradation can only be applied to geographically contiguous (i.e., continental) populations, taxonomists used an arbitrary assessment of the degree of difference to rank island populations (Stone 1899).

By the early twentieth century, the recognition of subspecies had degraded to the principle of “geographic representation.” Many thousands of distinctive and less distinctive taxa were combined in large polytypic species simply based on the non-overlap of their breeding ranges. The inclusion of subspecies into polytypic species was seen as a simplification of taxonomy, because it reduced the number of recognized species (Stejneger 1884; Mayr 1942). The effect on the number of bird species was substantial: within about 40 years, the number of recognized species had dropped from 18,939 (Sharpe 1909) to 8590 (Mayr and Amadon 1951).

By the mid-twentieth century, the number of bird species started to increase again, and this trend is accelerating (Fig. 2.2b). Increases of species numbers have also been documented in other vertebrates, but the rate of the increase differs among groups (Fig. 2.3). For instance, the number of extant bird species increased by 0.9%

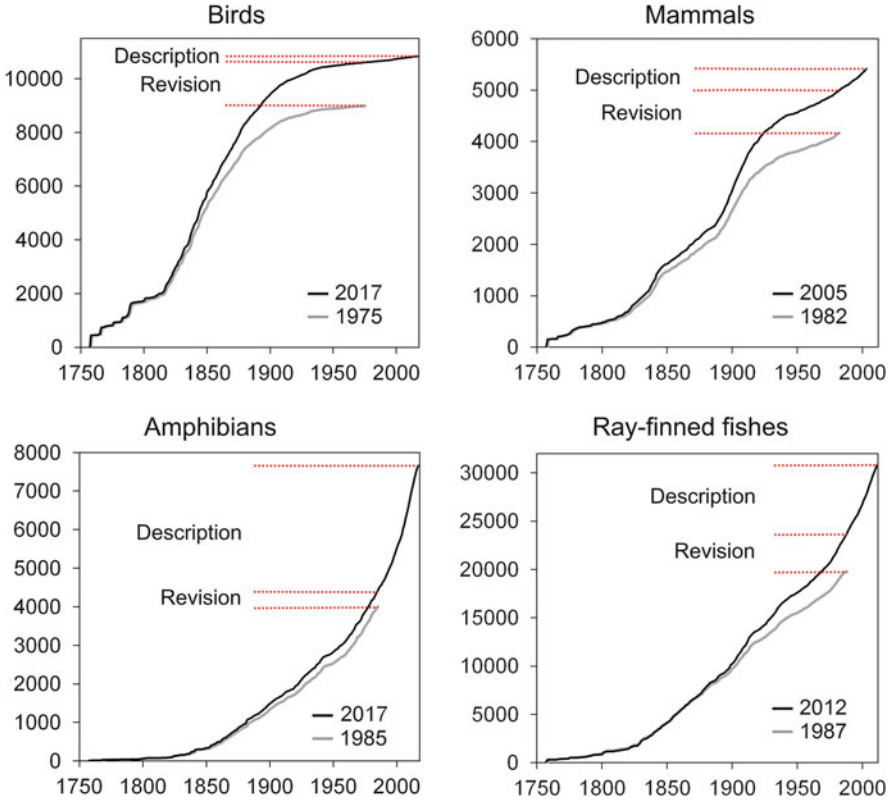


Fig. 2.3 Cumulative numbers of species of birds, mammals, amphibians, and ray-finned fishes recognized in classifications published in 1975–1987 (gray lines) and 2005–2012 (black lines). The relative contributions of taxonomic description (new species) and taxonomic revision (subspecies upgraded to species rank) differ greatly among vertebrate groups, with revisions predominating in birds and mammals and descriptions predominating in ray-finned Fishes and especially amphibians

per year during 2007–2016, whereas in amphibians the increase was a whopping 2.4% per year.

2.9 The Drivers of Taxonomic Change

Why does the number of bird species keep rising even after more than 250 years of taxonomic research? Three major reasons have been proposed for the increasing number of vertebrates recognized by specialists: (1) new discoveries, (2) revisions based on new empirical evidence (e.g., molecular data), and (3) revisions based on changes of the way species are delimited. Hanken (1999) attributed the increase of the number of amphibian species to all three of these, whereas Isaac et al. (2004)

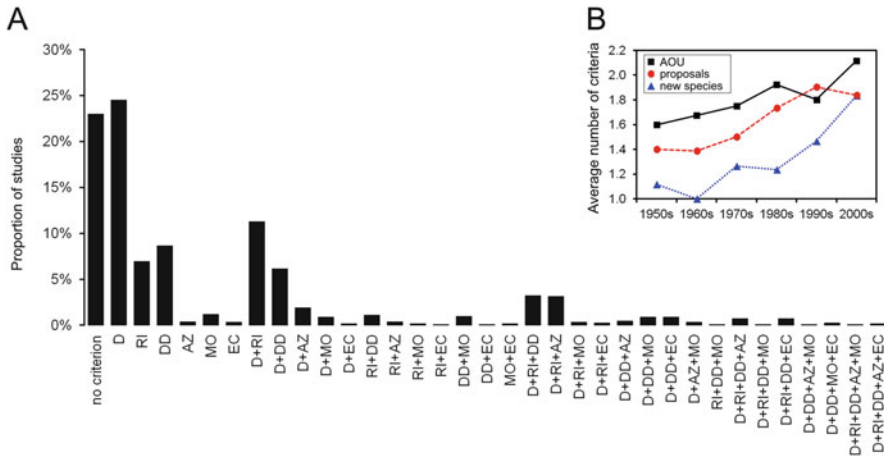


Fig. 2.4 (a) Species criteria used in a dataset of 1249 taxonomic studies (new descriptions, revisions, and recommendations made by the AOU Committee on Classification and Nomenclature) published between 1950 and 2009 (Sangster 2014). Note the large number of different combinations of criteria, illustrating the eclectic nature of species-level taxonomy in birds. *D* diagnosability, *RI* reproductive isolation, *DD* degree of difference, *AZ* adaptive zone, *MO* monophyly, *EC* exclusive coalescence of gene trees. (b) Changes in the average number of criteria per taxonomic hypothesis, illustrating the increasingly pluralistic nature of species delimitation (Modified from Sangster 2014)

incorrectly attributed the rising number of recognized species of birds and mammals to a shift toward the phylogenetic species concept (see below).

The relative role of descriptions and revisions in the increasing number of species is easily inferred by comparing plots of the cumulative number of species described over time of a recent classification with that of a less-recent classification (Fig. 2.3). These show that in birds, revisions play a much greater role in the increase than descriptions, whereas the opposite is true in amphibians (Fig. 2.3). More specifically, of the c. 92 species of birds that on average were added each year during 2007–2016, only about five per year were newly described species (Fig. 2.2b).

Analyses of the taxonomic literature have shown that the rising number of bird species cannot be attributed to a shift toward the phylogenetic species concept (Sangster 2009). The trend to recognize more species of birds started at least two decades before the introduction of the phylogenetic species concept, and most newly recognized species were not based exclusively on criteria associated with that concept (Sangster 2009). In a set of 747 taxonomic proposals published in major ornithological journals, about 85% of the newly proposed species were supported by new taxonomic data. Thus, in birds taxonomic revision is the predominant proximate driver of the growing number of species, and revisions are very often based on new empirical data.

Taxonomic practice is pluralistic (employing multiple types of evidence and criteria) and increasingly eclectic (employing many different combinations of criteria). Using a dataset of >1200 studies, a recent study found that six taxonomic criteria were applied in >30 unique combinations (Fig. 2.4; Sangster 2014). Avian

taxonomists apply different criteria as complementary rather than as rival approaches to species delimitation, which is consistent with the general lineage concept of species and with the methodological framework of integrative taxonomy (Sangster 2014). Another positive trend is that the information content of taxonomic studies is increasing; taxonomists write longer papers, use more characters and more specimens, make comparisons with more taxa, and make greater use of illustrations, sonagrams, and maps (Sangster and Luksenburg 2015). There is evidence that this promotes stability: more elaborate descriptions require fewer subsequent revisions (Sangster and Luksenburg 2015).

The great magnitude of the lumping process during the first half of the twentieth century and the nearly complete lack of empirical evidence that supported these revisions are important reasons why the taxonomy of birds is still in flux. Taxonomic changes since the 1950s have a strong empirical basis and thus mark progress. Furthermore, because numbers of recognized species of birds are increasing exponentially (Fig. 2.2b) and many bird species have not been revised since the early twentieth century, species inventories of birds are still far from complete.

2.10 Benefits of Integrative Taxonomy to Other Fields

2.10.1 Speciation Studies

The processes by which new evolutionary lineages diversify may be highly complex and may differ among species. Identifying the main processes involved in speciation typically requires in-depth study from multiple angles. Research questions asked in speciation research are often identical to those that taxonomists ask (e.g., In which ways do the populations differ from each other? What is their population structure? When did the populations diverge? Do members of these populations recognize each other as potential mates/competitors? Is there any hybridization and does this lead to gene flow?). Modern taxonomic studies are crucial for speciation research, because one must first document patterns of variation before one can identify and understand the processes responsible for these patterns. Indeed, many interesting case studies in speciation research recently have been identified from integrative taxonomic research, as the following examples illustrate.

The black Carrion Crow *Corvus corone* and gray-and-black Hooded Crow *C. cornix* have long been treated as subspecies, because they meet and hybridize along a narrow contact zone in central Europe and Scotland. A series of modern studies in their hybrid zone showed that the crows actually behave as species (reviewed by Parkin et al. 2003). Further research on mitochondrial and nuclear DNA divergence found almost no divergence at the DNA level (Haring et al. 2007, 2012; Wolf et al. 2010), indicating either very recent speciation or widespread gene flow or both. Building on this work, full-genome studies demonstrated that the Carrion and Hooded Crows indeed show widespread gene flow in large parts of their genome, but not in the genes responsible for mate choice (preference for

“black” vs. “gray-and-black” phenotypes) and plumage type. Both sets of genes are located rather close to each other and occupy a <2-megabase stretch of DNA (Poelstra et al. 2014). This shows that speciation may result from changes in a relatively small and local part of the genome. In turn, this finding is relevant for taxonomy, because it shows that gene flow does not necessarily falsify species rank and that traditional molecular methods (mtDNA and a few ncDNA markers) may not suffice to find all lineages.

Similarly, the discovery that two populations of *Oceanodroma* storm petrels in the Azores (Portugal) most likely originated through sympatric speciation by allochrony (Friesen et al. 2007) was preceded by a series of taxonomic studies which documented various aspects of their divergence. Storm petrels breeding during the summer (hot season) and those breeding during winter (cold season) were first found to show differences in morphology and timing of molt (Monteiro and Furness 1998). This was followed by studies which showed that these populations also differ by vocalizations, response to playback, and mtDNA and microsatellites but are more closely related to each other than to any other storm petrel (Bolton 2007; Friesen et al. 2007; Smith et al. 2007). The combined data provided compelling evidence that hot- and cold-season storm petrel populations arose sympatrically (Friesen et al. 2007). This represented the first evidence for sympatric speciation by allochrony in tetrapods.

Hybrid speciation is another rare form of speciation. Based on the descriptive taxonomic works of Meise (1936) and Johnston (1969), Italian Sparrow *Passer italiae* had long been suspected to be a hybrid species resulting from past interbreeding between Spanish *P. hispaniolensis* and House Sparrows *P. domesticus*. This was corroborated by recent work on morphology, microsatellites, and mitochondrial and nuclear DNA sequences (Elgvin et al. 2011; Hermansen et al. 2011, 2014; Trier et al. 2014). Conversely, these studies have helped clarify the taxonomic status of Italian Sparrow, which is now treated as a full species (Sangster et al. 2015).

2.10.2 Biogeography

Biogeography, the science that attempts to document and understand spatial patterns in biology, is one of the primary components of systematic research. Taxonomy (including phylogenetic study) provides the scientific basis for historical biogeography. Refinement of taxonomic designations results in increased precision in biogeographic studies. For instance, modern phylogeographic and taxonomic studies (Ribas et al. 2011; Fernandes et al. 2014) have not only corroborated the existence of multiple areas of endemism in the Amazon region of South America (Cracraft 1985) but also contributed to the designation of a new area of endemism northwest of Manaus, Brazil (Borges and da Silva 2012). Similarly, the importance of the white-sand forests of the northern Peruvian Amazon was only recently recognized due to the discovery of several new species confined to this habitat (Whitney and Alvarez Alonso 1998, 2005; Alvarez Alonso and Whitney 2001; Isler et al. 2002).

Contact zones have long been of interest for biogeographers, because these may help identify which ecological and historical factors have influenced the past and present distributions of populations and their divergence (Swenson 2010). Recent taxonomic studies have revealed several previously overlooked contact zones between morphologically similar taxa. Examples include the geese *Branta canadensis/hutchinsii* in Arctic North America (Paxinos et al. 2002), the pittas *Erythropitta macklotii/habenichti* in New Guinea (Irestedt et al. 2013), and the grey shrikes *Lanius excubitor/borealis* in Western Siberia (Olsson et al. 2010).

The processes responsible for high tropical species richness have attracted much debate, but with little consensus so far. For instance, it has been proposed that speciation rates in the tropics are higher or that extinction rates are lower or that clades originate in the tropics but only recently spread to higher latitudes leaving little time for species richness to accumulate in temperate zones (Pianka 1966; Rahbek and Graves 2001; Willig et al. 2003; Weir and Schluter 2007). Adequate, unbiased inventories of the diversity at different latitudes are an important first step in distinguishing among these and many other explanations. Recent phylogenetic and taxonomic research suggests that species diversity has been underestimated especially in the tropics (Lohman et al. 2010; Milá et al. 2012; Voelker et al. 2013), and this has bearing on some of the explanations that have been proposed for latitudinal diversity gradients (e.g., Tobias et al. 2008; Irestedt et al. 2013). Recognition of more species in the tropics results in steeper latitudinal gradients, but also in shorter branch lengths, suggesting more recent speciation (Irestedt et al. 2013).

2.10.3 Conservation

Taxonomy provides the scientific underpinnings of biodiversity conservation (Wheeler and Cracraft 1997; Cotterill et al. 2017). There are at least three major ways in which conservation work benefits from continued taxonomic research. First, the discovery and documentation of species lineages represents a crucial first step in biodiversity conservation, because species are often considered the basic currency in conservation (e.g., IUCN Red List). By documenting previously overlooked species and removing invalid species, taxonomic research helps conservationists prioritize their work. Threatened species which had remained hidden due to incorrect taxonomy are still being documented even in supposedly well-known parts of the world (Fig. 2.5), underscoring the urgency of taxonomic work.

Second, taxonomic research helps to delimit Endemic Bird Areas which are an efficient way to identify conservation priorities for restricted-range species (Stattersfield et al. 1998). An Endemic Bird Area is an area which encompasses the overlapping breeding range of at least two species that have a range of <50,000 km². Two examples of Endemic Bird Areas recently identified by taxonomic research are the Balearic Islands and Corsica. Until the mid-1990s, only one endemic species was recognized (Corsican Nuthatch *Sitta whiteheadi*), but subsequent taxonomic study has added two endemic species to the Balearic Islands (Balearic Shearwater *Puffinus*



			<u>After</u> <u>taxonomic revision</u>	<u>Before</u> <u>taxonomic revision</u>
	Population size	Area	IUCN status (2017)	IUCN status (2015)
	100-132 pairs	34 km ²	Endangered (<i>Fringilla polatzeki</i>)	Near-threatened (<i>Fringilla teydea</i>)
	1000-2500 pairs	760 km ²	Near-threatened (<i>Fringilla teydea</i>)	

Fig. 2.5 Taxonomic revision affects the recognition of threatened species. The Blue Chaffinch *Fringilla teydea* was long considered a polytypic species with two subspecies, *F. t. polatzeki* on Gran Canaria and *F. t. teydea* on Tenerife. Until 2016, Blue Chaffinch was classified as a “near-threatened” species, because the range size and population numbers of the Tenerife taxon (now *F. teydea*) overwhelmed those of the much rarer Gran Canaria taxon (now *F. polatzeki*). After two studies showed that the two taxa differed in plumage, morphometrics, vocalizations, response to playback, sperm morphology, and nuclear DNA (Lifjeld et al. 2016; Sangster et al. 2016b), *F. polatzeki* was classified as an endangered species. Photographs courtesy of Jolanda A. Luksenburg (upper) and Ian Merrill (lower)

mauretanicus and Balearic Warbler *Sylvia balearica*), one to Corsica (Corsican Finch *Carduelis corsicana*), and two which are shared between the two areas and parts of mainland Italy (Moltoni’s Warbler *Sylvia subalpina* and Mediterranean Flycatcher *Muscicapa tyrrhenica*) (Sangster 2000; Shirihai et al. 2001; Sangster et al. 2002; Brambilla et al. 2008; Förschler et al. 2009; Pons et al. 2016).

Finally, taxonomic revisions help identify the lineages that contain most evolutionary history, which is an important measure for prioritizing conservation efforts (e.g., Vane-Wright et al. 1991; Mooers and Atkins 2003). Using metrics that capture the evolutionary distinctiveness and conservation status of species, Jetz et al. (2014) identified the top-ranking bird species for phylogenetic conservation measures. Several of these represent species that have only recently been revealed by taxonomic study, including North Island Brown Kiwi *Apteryx mantelli* (Burbidge et al. 2003), Udzungwa Forest Partridge *Xenoperdix udzungwensis* (Dinesen et al. 1994), Australian Painted-snipe *Rostratula australis* (Baker et al. 2007), and New Zealand Storm Petrel *Fregatta maoriana* (Robertson et al. 2011).

2.11 Remaining Issues

Integrative taxonomy is an active field, and it is likely that various aspects will be further clarified and developed in the near future (Padiál et al. 2010; Schlick-Steiner et al. 2010). Among the issues that remain to be clarified are the following:

As noted before, one of the arguments for integrative taxonomy is that different kinds of evidence highlight different aspects of species divergence: the tempo of divergence, frequency of hybridization, adaptation, and the geography and mechanisms of speciation. But this also means that there will be more and more cases of discordance among different kinds of evidence. How should one deal with discordance? The most sensitive methods may not be the most accurate methods. On which grounds does one decide which hypothesis is most likely correct? Should one err on the side of recognizing too few or too many species (e.g., Carstens et al. 2013)?

Continued progress in taxonomy depends largely on the collection of new empirical data (including specimens, sound recordings, and DNA sequences). Obtaining sufficient data may be problematic in several cases, such as (1) recent speciation when many markers may not be sensitive enough to detect divergence, (2) in paleontology when data are typically limited to bone material, and (3) when species are known from very few specimens (e.g., singletons; Lim et al. 2012). Finding efficient ways to maximize confidence in taxonomic hypotheses will remain a major challenge.

Acknowledgments I am grateful to Jolanda Luksenburg and Ian Merrill for the permission to use their photographs of Blue Chaffinches. I was supported by grants from Mark Constantine and the Swedish Research Council (grant 2015-06455).

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Suggestion for Further Reading

- Ereshefsky M (ed) (1992) The units of evolution. MIT Press, Cambridge [a collection of classic papers in the debate over species concepts, written by biologists and philosophers of science]

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