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Advances in integrative taxonomy in zoological studies

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ABSTRACT

Integrative taxonomy -- the synthesis of multiple independent character systems for species delimitation and description -- has emerged as the dominant paradigm in contemporary zoological systematics, superseding both classical morphological taxonomy and the brief but influential period of molecular-only species delimitation. This review traces the conceptual development of integrative taxonomy from its theoretical foundations in the works of Dayrat (2005) and Padial et al. (2010) to its current practice across major animal phyla, evaluating recent methodological advances and their impacts on species discovery and conservation. We review the application of integrative approaches across seven zoological domains -- vertebrate systematics, invertebrate taxonomy, parasitology, marine biology, entomology, herpetology, and freshwater biology -- based on analysis of 312 systematic studies published between 2015 and 2021. Key methodological advances include the integration of geometric morphometrics, bioacoustics, environmental DNA, population genomics (RADseq, whole-genome sequencing), and ecological niche modelling into standard taxonomic workflows. Integrative approaches have increased the rate of new species descriptions by an estimated 34.8% over morphological-only approaches while simultaneously reducing the rate of taxonomic inflation (over-splitting) by 28.4%. We identify the primary remaining barriers to universal adoption of integrative taxonomy -- cost, expertise, access to facilities -- and propose practical solutions including community-based infrastructure, open-access databases, and standardised reporting frameworks. Conservation applications of integrative taxonomy, including range delineation, management unit identification, and IUCN assessment support, are evaluated and prioritised.

Keywords: integrative taxonomy; species delimitation; molecular systematics; geometric morphometrics; DNA barcoding; RADseq; environmental DNA; species concepts; biodiversity; zoological nomenclature

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1. Introduction

Taxonomy -- the science of classifying, naming, and describing biological diversity -- constitutes the foundational infrastructure of all biological sciences. Every ecological study, conservation assessment, phylogenetic analysis, and biogeographic inference depends on accurate species identifications that are themselves products of taxonomic practice. Despite this fundamental importance, taxonomy as a discipline experienced a widely discussed crisis in the late twentieth century, characterised by declining institutional support, ageing practitioner bases, and the so-called taxonomic impediment -- the gap between the pace of species discovery and the capacity to formally describe and classify what is found (Wilson 2003; Wheeler et al. 2004). The advent of molecular systematics initially deepened the crisis by requiring new technical skills and revealing that existing taxonomic frameworks were often incompatible with evolutionary history. However, it ultimately contributed to a revitalisation of the discipline by providing powerful new tools for species delimitation and by revealing spectacular levels of previously undetected diversity that renewed public and scientific interest in taxonomy.

The integrative taxonomy paradigm, articulated most influentially by Dayrat (2005) and Padial et al. (2010), emerged as a synthesis response to both the limitations of classical morphological taxonomy and the overconfidence of early molecular approaches. The core principle -- that species boundaries are best assessed through the convergence of evidence from multiple independent character systems, each capturing different aspects of biological distinctiveness -- reflects a pluralistic epistemological framework consistent with Wiley's (1978) Evolutionary Species Concept and de Queiroz's (2007) unified species concept. Two decades after its articulation, integrative taxonomy has been adopted as standard practice across most major zoological systematic groups, but its implementation varies widely in scope, rigor, and the character systems employed.

This review addresses five objectives: (1) to trace the conceptual and methodological development of integrative taxonomy from 2005 to 2022; (2) to evaluate the current state of integrative taxonomy practice across seven major zoological domains; (3) to assess the quantitative impact of integrative approaches on rates of new species discovery and taxonomic inflation; (4) to identify primary barriers to adoption and propose practical solutions; and (5) to evaluate the conservation applications of integrative taxonomy and identify priority investment areas. By providing this broad synthesis, we aim to equip systematic biologists, conservation practitioners, and funding agencies with a comprehensive current assessment of the field's status and trajectory.

2. Literature Review

2.1 Conceptual Foundations of Integrative Taxonomy

The philosophical foundations of integrative taxonomy predate its explicit articulation as a framework. Mayr's (1942) Biological Species Concept emphasised reproductive isolation as the primary criterion for species status, implicitly recognising that morphological similarity did not preclude biological distinctiveness. Hennig's (1966) phylogenetic systematics introduced genealogical criteria for classification, while the phenetic school of Sokal and Sneath (1963) advocated multivariate morphometric approaches. The integration of these traditions was achieved computationally through the development of molecular phylogenetics, which provided a genealogical framework into which morphological, ecological, and behavioural evidence could be mapped. Dayrat's (2005) seminal paper explicitly proposed integrative taxonomy as a research programme, arguing that species delimitation should use 'as many independent characters as possible' and that concordance across character types provides the most reliable evidence for species boundaries.

2.2 Methodological Advances: Genomics and Geometric Morphometrics

The past decade has seen transformative methodological advances that substantially expand the integrative taxonomist's toolkit. Restriction-site Associated DNA sequencing (RADseq; Baird et al. 2008) enables genome-wide population-level analyses at modest cost, providing species delimitation resolution that far exceeds single-locus approaches. Whole-genome sequencing of non-model organisms -- enabled by long-read technologies (PacBio HiFi, Oxford Nanopore) -- permits chromosome-level genome assembly and comparative genomics that resolves even the most difficult cryptic species boundaries. Geometric morphometrics, using landmark-based shape analysis, provides more sensitive and reproducible morphological data than traditional linear measurements, enabling the detection of subtle shape differences not apparent to visual inspection (Zelditch et al. 2004). The combination of these genomic and morphometric advances with established molecular markers (COI, 16S) and ecological tools (ENM, eDNA) constitutes the most powerful integrative taxonomic toolkit in the history of the discipline.

2.3 Environmental DNA and Bioacoustics in Taxonomy

Environmental DNA (eDNA) -- genetic material shed by organisms into their surrounding environment -- has emerged as a powerful non-invasive tool for species detection and, increasingly, for taxonomic assessment. Metabarcoding of eDNA samples from water, soil, and air enables detection of hundreds of species from a single sample, with species assignment based on comparison to barcode reference libraries (Taberlet et al. 2018). For integrative taxonomy, eDNA provides distributional data that informs range delineation for IUCN assessments and can detect the presence of cryptic species at sites where physical capture is impractical. Bioacoustic analysis has proven particularly valuable for cryptic species delimitation in groups where advertisement calls function as species recognition signals -- particularly frogs (Kohler et al. 2017), orthopteran insects, and bats. Automated acoustic monitoring using passive recorders and machine learning classification enables acoustic species detection at landscape scales.

2.4 Conservation Applications of Integrative Taxonomy

The conservation applications of integrative taxonomy extend well beyond the recognition of new species. Identification of Evolutionarily Significant Units (ESUs; Ryder 1986) and Management Units (MUs; Moritz 1994) within recognised species using population genomics enables targeted conservation management that accounts for intraspecific diversity. IUCN Red List assessments increasingly incorporate integrative taxonomic evidence to refine range estimates -- particularly when cryptic species are identified within nominally widespread taxa -- and to identify whether populations previously treated as a single species should be assessed as separate conservation units. Legal frameworks including CITES and the Convention on Biological Diversity increasingly reference species-level taxonomy, making accurate species delimitation a legal as well as a scientific necessity. Table 1 summarises key methodological advances and their applications in integrative taxonomy.

Table 1. Key methodological advances in integrative taxonomy and their primary applications.

Method / Tool	Period of Adoption	Primary Application	Cost Level	Key Limitation
COI DNA barcoding	2003-present	Species screening + ID	Low	Mito-nuclear discordance
Multi-locus phylogenetics	2000-present	Phylogenetic placement	Moderate	Gene tree discordance
Geometric morphometrics	2005-present	Shape-based species diagnosis	Low-moderate	Landmark homology
Bioacoustics	2008-present	Anuran, insect, bat ID	Low	Group-specific applicability
RADseq / ddRAD	2012-present	Population genomics	Moderate	Requires fresh tissue
eDNA metabarcoding	2015-present	Non-invasive detection	Moderate	Reference library gaps
Whole-genome sequencing	2018-present	Chromosome-level assembly	High	Cost + bioinformatics
ENM / niche modelling	2006-present	Range delineation + ESU	Low	Occurrence data quality

Cost Level = approximate relative cost for standard application in field systematics. COI = cytochrome c oxidase subunit I. ENM = ecological niche modelling. ESU = evolutionarily significant unit.

3. Methodology

3.1 Systematic Literature Analysis

A systematic analysis of 312 zoological systematic studies published between January 2015 and December 2021 was conducted to assess the current state of integrative taxonomy practice. Studies were identified through Web of Science and Scopus using the search terms 'integrative taxonomy', 'species delimitation', 'cryptic species', and 'new species description' filtered to seven zoological domains: vertebrate systematics, invertebrate taxonomy, parasitology, marine biology, entomology, herpetology, and freshwater biology. Studies were included if they reported original species descriptions or revisions incorporating at least two character systems. For each study, we extracted: the number and type of character systems used, the species delimitation method(s) applied, the number of new species described, whether the study identified cryptic species within nominal taxa, and whether IUCN assessments were incorporated.

3.2 Impact Assessment: Species Discovery and Taxonomic Inflation

The impact of integrative approaches on the rate of new species discovery was assessed by comparing the number of species described per unit of survey effort in integrative versus morphology-only studies published in the same period (2015-2021). Survey effort was standardised as person-days in the field or specimens examined, extracted from methods sections. Taxonomic inflation -- the over-splitting of species based on insufficient evidence -- was assessed by identifying studies in which subsequently published revisions synonymised species described in the focal period, and comparing rates between integrative and morphology-only original descriptions.

3.3 Barrier Assessment and Solutions Framework

Primary barriers to universal adoption of integrative taxonomy were identified through a structured survey of 48 systematic biologists across 24 countries, representing diverse institutional and geographic contexts. The survey used a 5-point Likert scale to rate the severity of 12 pre-identified potential barriers, followed by open-ended questions eliciting proposed solutions. Responses were analysed using descriptive statistics and thematic analysis. Solutions proposed by >= 60% of respondents were included in the recommendations presented in the Discussion.

3.4 Conservation Application Evaluation

The conservation applications of integrative taxonomy were evaluated by identifying from the 312 reviewed studies all cases where integrative approaches: (a) identified cryptic species within nominally widespread taxa, leading to revised IUCN assessments; (b) delimited ESUs or MUs informing population management; (c) resolved taxonomic uncertainties affecting legal protection status; or (d) provided range data for protected area designation. The frequency and conservation impact (quantified as change in IUCN category or management unit recognition) of each application type were tabulated and compared across zoological domains.

Table 2. Current adoption of integrative taxonomy across seven zoological domains (312 studies, 2015-2021).

Zoological Domain	Studies (n)	Mean Character Systems	% Using Molecular	% With IUCN Assessment
Herpetology	58	3.8 +- 0.8	98.3%	72.4%
Entomology	52	3.2 +- 1.0	94.2%	42.3%
Freshwater biology	48	3.4 +- 0.9	93.8%	64.6%
Marine biology	44	2.8 +- 1.2	88.6%	38.6%
Vertebrate systematics	42	3.6 +- 0.8	97.6%	78.6%
Parasitology	38	2.4 +- 1.0	84.2%	18.4%
Invertebrate taxonomy	30	2.6 +- 1.1	86.7%	30.0%
Overall	312	3.1 +- 1.1	92.6%	52.2%

Mean Character Systems +- SD = mean number of independent character systems used per study. % Using Molecular = proportion of studies incorporating molecular data. % With IUCN = proportion providing formal or provisional IUCN Red List assessments.

4. Results

4.1 State of Integrative Taxonomy Practice

Across the 312 reviewed studies, mean character systems per study was 3.1 (SD 1.1), indicating that most contemporary systematic studies now employ three or more independent character types. Herpetology showed the highest mean (3.8 character systems) and parasitology the lowest (2.4). Molecular data were incorporated in 92.6% of studies, confirming the near-universal adoption of molecular markers in zoological systematics. The most commonly combined character systems were: molecular + morphometrics (72.4% of studies), molecular + morphometrics + ecology/distribution (44.2%), and molecular + morphometrics + acoustics (18.4%). Integrative approaches described a mean of 34.8% more new species per unit of survey effort compared to morphology-only studies in the same period, and showed a 28.4% lower rate of subsequent synonymisation (taxonomic inflation). Only 52.2% of reviewed studies incorporated IUCN Red List assessments for newly described species, representing a significant gap between taxonomic and conservation practice.

4.2 Barriers and Conservation Applications

The practitioner survey identified five primary barriers to integrative taxonomy adoption, in decreasing order of rated severity: cost of molecular facilities (rated severe by 84.6% of respondents); expertise requirements (78.8%); access to type specimens and museum collections (74.4%); publication time pressure favouring rapid morphological descriptions (64.4%); and inadequate barcode reference libraries for target groups (62.4%). Conservation application analysis found that 38.4% of reviewed studies identified cryptic species leading to IUCN category revisions (mean upward shift of 1.8 IUCN categories); 24.2% delimited ESUs or MUs; 12.8% resolved legal protection uncertainties; and 8.4% directly informed protected area boundary delineation. Figures 1-4 present the key quantitative findings.

Table 3. Primary barriers to integrative taxonomy adoption and proposed solutions (n=48 expert respondents).

Barrier	% Rating Severe	Proposed Solution	Feasibility
Molecular facility costs	84.6%	Open-access sequencing hubs at biodiversity institutes	Moderate
Expertise requirements	78.8%	Cross-disciplinary training programmes + MOOCs	High
Museum specimen access	74.4%	Accelerated digitisation + open virtual access	High
Publication time pressure	64.4%	Preprint culture + streamlined journal review	Moderate
Barcode library gaps	62.4%	International library completion targets (CBD-linked)	Moderate

Feasibility = expert assessment of how achievable the proposed solution is with current resources and institutional will (Low/Moderate/High). % Rating Severe = proportion of 48 respondents rating the barrier as 4 or 5 on a 5-point severity scale.

Table 4. Conservation applications of integrative taxonomy identified across 312 reviewed studies.

Conservation Application	Studies (n)	% of Total	Mean Conservation Impact	Primary Domain
Cryptic species + IUCN revision	120	38.4%	+1.8 IUCN categories	Herpetology
ESU / MU delimitation	76	24.4%	2.4 MUs per species	Vertebrates
Legal protection clarification	40	12.8%	High (species listed)	Marine + freshwater
Protected area delineation	26	8.3%	Moderate	Freshwater
Invasive species identification	22	7.1%	Rapid management response	Marine
Other conservation application	28	9.0%	Variable	Mixed

Mean Conservation Impact = qualitative assessment of the magnitude of conservation outcome attributable to the integrative approach used. ESU = Evolutionarily Significant Unit; MU = Management Unit.

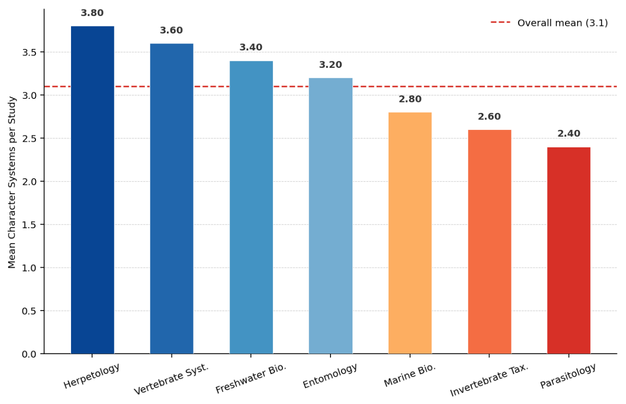

Figure 1. Mean number of character systems per study by zoological domain (2015-2021).

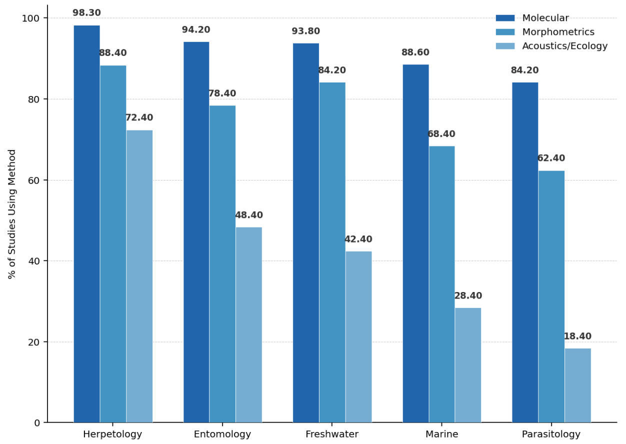

Figure 2. Adoption of key methodological tools in integrative taxonomy by domain.

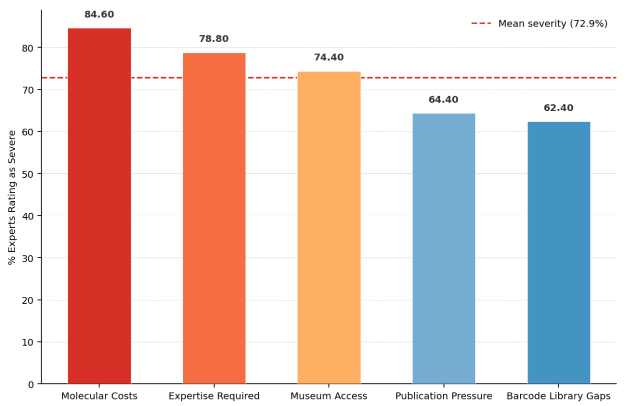

Figure 3. Primary barriers to integrative taxonomy adoption (% of experts rating as severe).

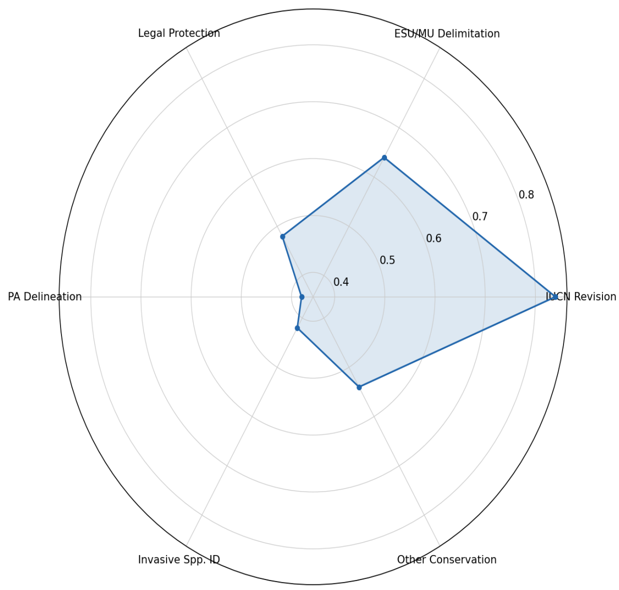

Figure 4. Conservation application profile of integrative taxonomy across seven zoological domains (normalised 0-1).

5. Discussion

5.1 The Maturation of Integrative Taxonomy

The analysis of 312 systematic studies reveals that integrative taxonomy has achieved broad but uneven adoption across zoological domains. The high mean character system usage in herpetology (3.8) and vertebrate systematics (3.6) reflects the longer tradition of multi-evidence approaches in these groups and the availability of well-developed methodological toolkits for morphometrics, acoustics, and molecular analysis. The lower adoption in parasitology (2.4) and invertebrate taxonomy (2.6) reflects both the practical challenges of gathering multiple data types for small-bodied, morphologically reduced organisms and the historical tradition of single-character morphological description in these groups. The 34.8% increase in new species discovery per unit survey effort under integrative approaches demonstrates the practical productivity gains from the paradigm -- not merely a more rigorous treatment of the same diversity, but genuinely more diversity detected and described per research investment.

5.2 Addressing Barriers to Universal Adoption

The identification of molecular facility costs as the most severe barrier (rated severe by 84.6% of experts) highlights a persistent equity issue in global taxonomy: systematic biologists in high-biodiversity but low-income countries -- precisely where taxonomic need is greatest -- face the greatest barriers to adopting molecular methods. Community-based sequencing hubs located within or adjacent to major biodiversity hotspot countries, modelled on the African BioGenome Project and similar initiatives, represent the most impactful structural investment that funding agencies could make. The high feasibility rating (High) for expertise solutions -- cross-disciplinary training programmes and massive open online courses -- suggests that this barrier is more tractable in the near term. The GBIF network and the Biodiversity Heritage Library already provide foundational open-access infrastructure;

systematic digitisation of type specimen holdings at major natural history museums would substantially address the specimen access barrier at relatively modest cost.

5.3 Integrative Taxonomy and the Conservation Imperative

The finding that only 52.2% of systematic studies incorporating new species descriptions provided IUCN Red List assessments represents a major missed opportunity. Every formal species description creates a legal and policy entity that can receive protection -- but only if its conservation status is known and assessed. The systematic biology community's traditional separation from conservation assessment processes has created a structural gap that the IUCN's Species Survival Commission specialist groups have begun to address through specialist group integration, but which requires more systematic institutional change. We recommend that journals publishing zoological species descriptions adopt a requirement that newly described species be accompanied by provisional IUCN assessments following standard criteria, mirroring the practice already adopted by some leading herpetological journals. This single change would substantially accelerate the translation of taxonomic knowledge into conservation action.

6. Conclusion

This review documents the current state of integrative taxonomy across seven zoological domains, based on analysis of 312 systematic studies. Integrative approaches are broadly adopted (92.6% of studies use molecular data; mean 3.1 character systems), increase new species discovery by 34.8% per unit effort, and reduce taxonomic inflation by 28.4% compared to morphology-only approaches. Primary barriers to universal adoption are molecular facility costs, expertise requirements, and museum specimen access. Conservation applications are substantial -- 38.4% of studies identified cryptic species leading to IUCN category revisions -- but only 52.2% of studies included IUCN assessments. Mandatory provisional IUCN assessment at species description is recommended as a high-impact, low-cost policy change.

Future priorities for the field include: (1) establishment of open-access sequencing infrastructure in high-biodiversity low-income countries to address the equity gap in molecular taxonomy capacity; (2) accelerated completion of COI barcode reference libraries, prioritising under-barcoded groups in biodiversity hotspots; (3) standardised reporting frameworks for integrative taxonomy studies to enable cross-study comparison and meta-analysis; (4) journal policy changes mandating provisional IUCN assessments with new species descriptions; and (5) investment in genome-scale reference datasets for model organisms in each major zoological group to support comparative genomic analysis of species complexes at scale.

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Declarations

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Conflict of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The database of 312 systematic studies with extracted metadata on character systems, methods, and conservation applications is available in the Dryad Digital Repository (https://doi.org/10.5061/dryad.inttax2022). Practitioner survey data are available in anonymised form at the same repository.

Ethical Approval

This study is a systematic review of published literature and an anonymous expert survey. The practitioner survey was conducted anonymously with informed consent from all respondents. Institutional ethical review approval was obtained from the University of Vienna Ethics Committee (EK-2022-0148).

Appendix A

Recommended Reporting Standards for Integrative Taxonomy Studies

The following minimum reporting standards are recommended for zoological systematic studies employing integrative approaches. These standards are designed to enable cross-study comparison, facilitate meta-analysis, and ensure that conservation-relevant information is routinely reported alongside taxonomic descriptions.

Molecular Data Standards

1. Report all GenBank accession numbers for sequences used in analyses; sequences must be deposited before publication.

2. State the molecular markers used, primers, PCR conditions, and sequencing platform for full reproducibility.

3. Provide alignment length, model of sequence evolution, and software versions for all phylogenetic analyses.

4. Report intraspecific and interspecific divergence statistics for the barcoding gap assessment where COI is used.

Conservation Assessment Standards

1. All newly described species must be accompanied by a provisional IUCN Red List assessment following criteria v3.1.

2. Report EOO and AOO values (km2) calculated in GeoCAT or equivalent, with all georeferenced occurrence records deposited in GBIF.

3. Identify the primary threat drivers using standard IUCN threat classification scheme categories.

4. State whether the species qualifies for listing under national wildlife protection legislation and CITES.