

ESSENTIALISTIC PLURALISM: THE THEORY OF SPATIO-TEMPORAL POSITIONING OF SPECIES USING INTEGRATED TAXONOMY

Maxwell, S. J.¹, Congdon, B. C.^{1,2} & Rymer, T. L.^{1,2}

¹ *College of Science and Engineering, James Cook University, PO Box 6811, Cairns, Queensland, Australia*

² *Centre for Tropical Environmental and Sustainability Sciences, James Cook University, PO Box 6811, Cairns, Queensland, Australia*

Corresponding author email: stephen.maxwell@my.jcu.edu.au

Keywords: kind, essence, essentialism, evolution, species taxonomy

The resurrection of essentialist arguments, in the context of the modern evolutionary synthesis, highlights the need for a break from historical definitions of ‘kind’ and ‘essence’ in order to bring a new paradigm in which these terms are used to conceptualise and understand evolutionary processes. The definition of ‘essence’ is herein divided into two distinct parts, namely the structural essence, which is mutable and has an evolutionary context; and the character essence, which is the immutable spatio-temporal expression of the structural essence of an individual. In contrast, the ‘kind’ is herein redefined as a region within a wider phylogenetically constrained organism state that reflects a conflux of character essences that form an immutable semaphoront. This organism state enables the hypothetical delineation of spatio-temporally immutable forms, called species, which are drawn from an evolutionary continuum. These revised definitions and the taxonomic clades derived from them determine the species that are used in the construction of phylogenies that reflect true historical and evolutionary relationships between organisms. The use of integrated taxonomy allows taxonomists to choose the appropriate concept enabling the evolutionary significance of the organism to be explained. This refocuses the argument from the concept back to the criteria, but often at the cost of causal explanation or conceptional explicitness. While integrated taxonomy allows the taxonomist the freedom to delineate species outside of any rigid conceptual framework, we seek to apply to this freedom a limit to the understanding of the evolutionary potential of an organism through the framing of that organism in a fixed spatio-temporal point. We call this confined potential the ‘essence matrix’, and it is these boundaries of this matrix that define the evolutionary potential of past and future forms, as well as define and restrict the field of morphospace upon which convergence and reticulation of taxa can occur. We name this limitation on evolutionary potential, the essentialist arguments used to construct it, and the integrated taxonomic approach to criteria selection, ‘essentialistic pluralism’. Finally, we will examine the complexity of species demarcation, noting the continuing failure for explicitness in conceptual application even if criteria are obvious.

INTRODUCTION

The natural world is classically ordered according to hierarchical relationships that are constructed in a manner that does not reflect modern evolutionary principles and the new biological essentialist paradigm. The historical pursuit of inferring the natural relationships between organisms is primarily a by-product of human intellectual inquisitiveness and reflects a pseudo-theological search for understanding the natural order of life, a quest that has challenged philosophers and those interested in the sciences before the Common Era (Henry, 2011; Lewis, 1963). As scientific understanding and shifts in theological

influence have changed over time, so too have the processes and doctrines underpinning methodical approaches among those disciplines concerned with finding an optimal system of nomenclature similarly changed (Moritz, 2013).

The shift from theocratic creationism towards an evolutionary necessity in taxonomy has challenged the hierarchical orthodoxy conceptualised and instituted by Linné (1735, 1758). This challenge has led to conflict and a rigorous defence of systems of nomenclature based on personal ideology rather than theoretical optimisation (Brummitt, 2002; Cantino et al., 1999). Irrespective of the ideological stance taken, any system

of nomenclature needs to impart a sense of ontology, or reality, as well as to possess an inherent epistemology that enables a delineation of how derived taxonomic conceptual entities reflect the taxonomic needs of the classifier (Szalay & Bock, 1991). Consequently, taxonomists are drawn towards particular taxonomic schools of thought based on their personal understanding of evolutionary theory, taxonomical needs and predisposition towards an ideological stance on a particular taxonomic or species concept (Cracraft, 1987).

In order to re-engage the wider scientific community in the species debate, there needs to be an acceptance that the term 'species' has fundamentally differing meanings (Schlick-Steiner et al., 2019). The use of integrated taxonomy, with its unrestricted approach to conceptualisation of what is a species, allows the taxonomist the freedom to express a unique approach to exploring phylogeny without the shackles of rigid necessity to declare adherence to a single species concept (Yeates et al., 2011; Pavan & Marriog, 2016; Solari et al., 2019; Pardo-Diaz et al., 2019). The broader scientific community can be brought back to the species debate only when there is an acceptance that there is no correct or incorrect conceptuality in species definition, with all proposed species concepts theoretically having a usefulness (Schlick-Steiner et al., 2019). Many scientists have avoided species debates in evolutionary biology as a consequence of the semantics surrounding many of the current issues (Noor, 2002; Pante et al., 2015). Much of this avoidance can also be attributed to conceptual misunderstandings and ignorance of the theoretical basis for what actually constitutes a species. The broader scientific community can be brought back to the species debate only when there is an acceptance that because they are hypothetical there is no correct or incorrect conceptuality in species definition, with all proposed species concepts theoretically having usefulness (Hausdorf, 2011).

Species need to be conceptualised outside of taxonomic classificatory systems as they fall outside of systematic hierarchical arguments, being fundamentally hypothetical (Dubois, 2011). Although hypothetical in nature, a species hypothesis is represented by a set of real organisms. Thus, because species are real entities and not just intentional meanings derived by the taxonomist, they differ innately from higher classifications which are subjective in that there is no physical representation of the hypothetical rank (Ghiselin, 1974; Hull, 1976). This raises a point of contention: if species are real, why are many of the concepts that are used to define them based on unreal or non-causal criteria?

This leads to a complexity in conceptual realisation and invariably to conceptual misunderstanding, a problem again absent in higher taxonomic arguments that have no physical reality (Stamos, 2003). There is a need for criteria to give a sense of a touchstone to the real.

One of the problems with engaging a taxonomist in the species conceptual debate is that they are often at a loss to explain their meaning of species, falling into the trap of conceptual adherence and associated rhetoric and overlooking the hypothetical nature of the reference point in nature they seek to demarcate. Such rigidity to a conceptual belief invariably ends with the taxonomist at a loss when faced with contra-arguments (Hey, 2001). This adherence to a conceptual framework also loses sight of the primary mission of the taxonomist, which is, according to Mayden (1999, p. 115), "to discover, describe, and classify biological diversity, regardless of how much there may really be out there". It is also irrational for a taxonomist to bind him/herself to any concept due to its convenience in application or acceptance by the wider collective scientific community (Nadachowski, 1993). Further, the long-term species debate has failed to enunciate the significance of the nuances of the species concept applied by the practising biologist. The application of species concepts is used to make critical decisions that affect universal biodiversity and macroecological assessments, as well as provide the support for evolutionary understanding in fields well apart from the narrow frame of their activities (Hey et al., 2003; Tan et al., 2008; Naomi, 2011; Frankham, et al. 2012). This has never been more relevant than in contemporary taxonomic practice, with the rise of conservation-orientated systematic arguments which seek to limit the ability of the taxonomist to undertake wide-ranging revisions, with such revisions seen as a threat to global diversity (Garnett & Christidis, 2017; Thomson et al., 2018; Gangloff, 2019).

Taxonomic descriptions of new species are often fundamentally flawed as there is generally no explicit statement of the species concept used to delineate the taxon (Tan et al., 2008). This lack of conceptual explicitness leads invariably to three primary errors in the systematic demarcation of species:

- 1) Type I errors occur when there has been an overestimation of the number of species within a particular organism complex;
- 2) Type II errors occur when the number of species in the organism complex has been underestimated; and

3) Type III errors occur when there has been a misrepresentation of the systematic relationships between the organisms within the complex (Adams, 1998). This has serious implications for understanding evolutionary history, where “irrational” species could lead to a misrepresentation of the evolutionary progression of a clade (Adams, 1998), or in the conservation of endangered organisms (Garnett & Christidis, 2017).

When determining a species, a taxonomist has an obligation to nominate the species conceptual approach being followed, to ensure a clear understanding of the criteria that are necessary and sufficient to determine the population (Hausdorf, 2011). The need for explicitness in criteria brings the theoretical problem of species recognition back within the scope of the rules of nomenclature that govern the application of names (Knapp, 2008). In addition, the taxonomist has an obligation to inform on the actual process of speciation that has taken place, giving insight into the ontology and causation of organismic differentiation (Miller, 2001; Losos & Glor, 2003). The use of integrated taxonomy enables the taxonomist the freedom to choose species criteria that are most appropriate for the set of organisms, irrespective of definitions that may have been applied to their sister taxa. However, this freedom in descriptive modality needs to be coupled with conception explicitness, that is, not just state the method used to discriminate a taxon, but answer the causal question as well.

In this paper, we redefine ‘biological essentialism’ through the differentiation of the two concepts of ‘kind’ and ‘essence’ that have become erroneously synonymised in modern evolutionary theory. In addition, we will demonstrate that a ‘kind’ is a part of

an organism state, which is a fixed, discrete entity within a spatio-temporal framework that is defined by essences. The edges of the organism state represent the phylogenetically constrained boundaries of an organism at a particular point in time. Further, we will consider the pluralist approach to understanding what constitutes an ‘essence’, that is, the integrative taxonomic freedom to determine the criteria or species delimitation, and specifically describe two discrete forms of essence, namely the ‘character essence’ (Box 1), which is a spatio-temporally fixed character, and the ‘structural essence’ (Box 1), which is mutable and has an evolutionary context, a distinction that has yet to be fully explored within the literature. We present the ‘essence matrix’, which confines the organism state to a discrete boundary of evolutionary potential for an organism to reticulate and evolve within through time. Further, this paper will demonstrate that essentialistic pluralism is a standard for universality and addresses the need of species demarcation at its core: what is the intended meaning imparted by naming an organism and not just the criteria used to describe and differentiate it?

ESSENTIALIST TAXONOMY

Essentialism has a valuable role to play in providing an understanding of evolutionary processes as it explains the evolution of both the intrinsic and extrinsic natures of taxa (Walsh, 2006). Understanding the dualistic nature of taxa requires an acceptance of the evolutionary reality that organisms evolve subordinate monophyletic groups that have an ancestry determined by the linking of real organism states (Box 1) and not some evolutionary ideology (Brundin, 1972). Organism states are, in turn, defined by ‘kinds’ (Box 1), which are created by the congruence of ‘structural essences’ (Box 1).

BOX 1. Glossary of new and revised significant taxonomic terms.

Organism state: The phylogenetically constrained boundary of all potentially expressed essences that a biological population (considered a species) exhibits at a static point in its spatio-temporal evolution, that is, a holomorph.

Kind: A region within an organism state that represents a conflux of an organism’s structural essences, and reflects the nature of an organism at a point in its evolutionary progression; an immutable semaphoront.

Structural essence: An evolutionary trait that may represent a phenotypically plastic form, or an ecological boundary, which defines an intrinsic or extrinsic aspect of the organism.

Character essence: The immutable attribute of an individual that reflect a spatio-temporal expression of structural essences.

Essence matrix: The entire collection of structural essences that unifies the ancestral and descendant taxa and is used to define the higher clade from which an organism state has evolved, and bounds that organism’s potential for evolutionary divergence in form into the future.

'Kind' and 'essence' have often been used interchangeably although they are different concepts. Consequently, they have been maligned in the arguments against immutability that have been used to support the drive towards neo-Darwinism and the modern evolutionary synthesis (Mayr, 1987; Amundson, 1998; Okasha, 2002). There has been considerable debate on the nature of what actually constitutes an 'essence'. We make six observations. First, historically, to taxonomists such as Linné, the term essence simply meant that which is taxonomically useful (Winsor, 2006). Second, many contemporary essentialist arguments are pseudo-Aristotelian, based on either shared salient morphology, or innate intrinsic properties that have explicit and rigid taxonomic meaning (Wallace, 2002; Oderberg, 2007). Third, the essence of an organism has also been linked to its genotype, which is then expressed in the observable morphological, physiological or behavioural characters it displays (Kitts & Kitts, 1979). Fourth, the genotypical approach has been further refined into the extended phenetical approach, where the definition of essence includes ancestry and relational biology (Walsh, 2006; Elder, 2008). Fifth, the more minimalist approach to defining the essence, based on a character trait, is outside historical necessity and is not intrinsic to the definition of an individual (Dumsday, 2012). Finally, in contrast, the phylogenetic approach seeks to shift the focus of essentialism from a categorical basis to a more historical one, thus enabling the essence to be used in evolutionary biology through the incorporation of intrinsic with extrinsic, or relational essences as part of a wider holistic view of the organism (Devitt, 2010; Dumsday, 2012). Irrespective of the approach taken to defining the essence, one of the failings of these theories is the inability to differentiate between two distinctive essence forms, namely the structural and character essences.

The structural essences of an organism state arise from the collective essence matrix, which defines the morpho-space of inclusivity of the higher taxonomy to which the organism, in all possible phenotypically plastic forms and ecological boundaries, belongs. This organism state can be viewed simply as the boundary of a species' variability at an exact point in space and time; that is, a species is a fixed cross-section of a continuum chosen by the taxonomist to give a reference point to advance an explanation of the observable natural world. In contrast, the character essences are the immutable attributes of an individual and the spatio-temporal expression of the structural

essences at the point at which the species is circumscribed. Importantly, it is the character essences of a taxon that are used to provide the restricted definition of the kind within the broader organism state and are used to formulate the diagnosis of a species.

In the current essentialist debate, the concept of a 'kind' refers to an immutable form and is not linked to a particular end point in the hierarchical tree typology. Therefore, it is theoretically incorrect to refer to species in the classical sense in terms of discrete classes of natural kinds with an implicit immutability. Rather, species should be viewed as distinct representatives along a continuum, thus being evolutionarily plastic, rather than temporally variable. Kinds need to be viewed in terms of a convergence of structural essence axes within the organism matrix that enables the discernment of a collective type with an explicit taxonomic definition, albeit at the arbitrary judgement of the taxonomist (Forey, 2002). In this context, kinds represent the collection of units of change within an organism state that results from the subjective assessment of the unbroken chain of divergence (Dobzhansky, 1935). The kind forms a statement of evolutionary position chosen by the taxonomist to reflect a more inclusive organism state comprised of evolving structural essences.

Mayr (1987) rejected kinds, arguing that natural kinds were sterile, and consequently, this terminology should be restricted to inanimate objects, such as metals. However, this is an incorrect assumption based on an innate restrictiveness and lack of historicity that has been applied to the classical definition of a kind. Further, Mayr's approach is a rejection of the premise that species are capable of evolving, which is not upheld under the revised definition.

HISTORICAL PERCEPTIONS OF SPECIES

Darwin (1859) argued that species are arbitrary constructs of convenience selected from a fluctuating evolutionary pond of forms. This argument mirrors the belief that species are not discrete, but rather become indistinguishable within a merging metapopulation, where essences reticulate between individuals as populations (Lamarck, 1801). This idea was extended in the adaptive field theories of Wright (1932) and Dobzhansky (1951) in which discernment of taxa occurs at topological peaks of adaptational success. The valleys between the combination of genes indicate a point at which discrete organisms can be delineated from one another (Dobzhansky, 1951). Species, therefore, are hypothetically derived

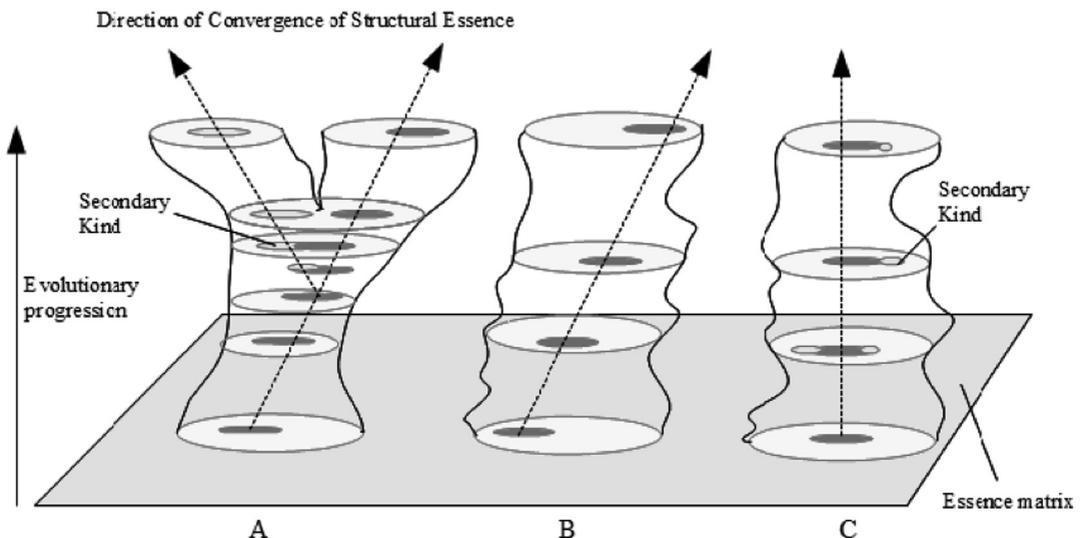
with the choice of demarcation, a decision made by the taxonomist.

The determination of a method to demarcate species has been a complex argument that has lasted centuries. Species need to be contextualised as a direct and discernible product of evolution constructed on a set of unifying essences chosen by the taxonomist. This currently occurs under guides of a theoretical concept chosen by the taxonomist. It is worth noting that the word species *sensu stricto* has two primary uses: it is used by taxonomists to delineate the forms within nature and create hypothetical hierarchies and, at the same time, it is used as a definition by the taxonomist to form a discernible immutable kind that acts as a hypothetical name-bearing reference point from which the process of evolution can be described (Mayr, 1987, 1996; Ereshefsky, 1992; Pleijel & Rouse, 2000). However, a species has a unique history and forms the more inclusive individual taxon with characteristics that are often not exhibited by the kind (Mishler & Donoghue, 1982; Nixon and Wheeler, 1990; Wiley, 1980). In contrast, higher taxa are multidimensional, existing within a spatio-temporal continuum in which the shared characteristics, or structural essences, are acting as axes that reflect their unique evolutionary direction (Andersson, 1990;

Szalay & Bock, 1991). When these axes converge, there is a forming of a discrete kind that can be given a formal definition (Dupré, 1981). Further, it is the relationships and clustering of these organism states based on shared ancestry that form the basis for the definition of higher taxa.

The birth of a new species, or delineation of two taxa, occurs in two ways. First, via the process of heterochronic cladogenesis, where two distinctive convergences arise in the organism state and the cleavage of new identifiable species with new identified phylogenetic constraints is deemed appropriate by the taxonomist (Huxley, 1957; Gould, 1977; Aze et al., 2013). Second, via the process of anagenesis, where a particular set of essences consistently converge outside the parameters of the parental metapopulation, as defined by the kind, requiring a redefinition of the kind (Huxley, 1957; Aze et al., 2013). While the acceptance of stasiogenesis implies that there is no multiplication of species and evolutionary failure, it may also reflect internal reticulation of the kind that reflects a convergence about a conflux of evolutionary optimisation (Huxley, 1957; Crusafont-Pairó & Truylos-Santonja, 1958; Figure 1). This reticulation has significant implications for phylogenetic reconstruction where only one gene has been utilised and the results may reflect only

FIGURE 1. The use of structural essences and the organism state to illustrate how the delineation of a kind can reflect modes of evolutionary phylogenesis: A) cladogenic evolution, in which there are two distinctive kinds created, each with individual phylogenetic constraints; B) anagenic evolution, where there is a shift in the structural essence convergence giving rise to distinctive changes in the kind within the relatively constant phylogenetic constraints; and C) stasiogenic evolution, in which there is no change in the kind, illustrating also that, while the phylogenetic constraints remain relatively stable, there may be reticulation.



gene evolution rather than the true state of the historical relationships between organisms. Evolution is more than the addition or subtraction of genetic material, but rather reflects an interaction of gene systems: the transitional valleys between gene clusterings represent taxic exploration of evolutionary possibilities rather than the initial stages of a genetic conflux giving rise to a new taxon (Dobzhansky, 1951).

Notwithstanding the mode of speciation, there is a necessary need for the generation of artificial temporal evolutionary stasigenesis for the delimitation of an organism state for the purposes of generating systematic understanding. This artificial stasiogenesis introduces an explicitness into the definition of species that then enables the production of real propositions on the historicity of the evolution of organisms. Taxa are explicitly defined in terms of kinds to avoid ambiguity and facilitate effective communication of the biological entity, reflecting the convergences of the axes even if these kinds are only representative of the wider, more-inclusive organism state (Dupré, 1981; Bryant, 1996). In point of fact, kinds represent nothing more than the adaptive peaks of an organism state.

Avise et al. (1987) highlight the complexity of gaining an understanding of the evolutionary significance and determining within an organism state when, from the extrapolation of a number of micro-evolutionary events, macroevolution is said to have occurred. Avise et al. (1987) saw macroevolutionary patterns as a substrate that is formed by the branches and twigs of intergenerational pedigrees within the complexity of phylogeny. One of the major theoretical standards for the delineation of a species from the myriad of branching possibilities is the simultaneous establishment of joint possession of structural essences, or synapomorphies, in each line (Bremer & Wanntorp, 1979). However, strict adherence to this method of differentiation has been found to be problematic in delineating when a novel structural essence, from the time of origin to fixation, gives rise to a new kind in a spatio-temporal organism state. This can be resolved by the defining of ancestry in terms of the absence of structural essences. However, the problem with this approach to the delineation of ancestor-descendant relationships lies in determining the temporal points of divergence, or when an adaptive peak deserves taxonomic isolation from its sister peaks. A particular characteristic may be more frequent in one taxon than another, absent altogether, or cryptic; and an assumption is made by the taxonomist practising a level of pattern cladistics when a new

species has arisen (Brady, 1982). If this is accepted, then it is the taxic homologies, which are based on descendants rather than transformational homologies, that are defining the phylogeny rather than just seeking to explain the genealogy.

Taxonomists also must deal with a level of contingency in delineating taxa (Chambers, 2012). There is a level of inference, based on evidence at hand that is used to generate the essences that define the organism state and then are restricted further into the kind. This involves a shift from a search for differences to an examination of commonality and the seeking of sub-patterns, or character essences, which form the conflux of axes unifying them (Kitcher 1981). The determination of which essences form the best guide to the determination of an organism state and the kind is a matter of relational taxonomic subjectivity (Okasha, 2002; Devitt, 2008). This reflects the reality that structural essences are innately ambiguous, comprised of an unknown number of transitions, possess an often-cryptic single origin, and may have undergone a level of evolutionary reversal (de Pinna, 1991). Therefore, the approach taken in the determination of a discrete kind, which represents a wider organism state, will be highly dependent on the species conceptual approach that is being utilised by the taxonomist. Again, it is worth noting that the conceptual approach to species is often restricted by a rigid adherence to an ideological stance that blinds the taxonomist to the real phylogeny.

There is a plethora of rigid methodological approaches enabling discrimination of the kind. Many of these methodical approaches to species conception are based on the single individual and are mereologically formulated, and all have the underlying drive to find exclusivity in definition (Hull, 1980; Kornet, 1993; de Pinna, 1999). This gives rise to the problem faced with the defining of the evolutionary unit and the nature of a species itself. Further, this problem can be reduced to one of taxonomic demarcation of inclusiveness once separation based on the components of the organism is used to aggregate and generate the populations (Hull, 1980). Notwithstanding the need for definitional exclusivity, species can also be considered as a set of organisms with a unique relationship that forms a natural heterogeneous individual (Kitcher, 1984a; Ereshefsky, 1992).

Irrespective of the species concept that is chosen by the taxonomist, there are four basic characteristics that must be met in order to fulfil the needs of communication of the natural world. First, there needs to

be a reality, or an actual spatio-temporal existence, even if this is unobservable (Cracraft, 1987). Second, the species needs to have a level of individualisation and mutual exclusivity, enabling a demarcation of it from other organisms (Cracraft, 1987; Kornet, 1993). Third, there needs to be irreducibility, such that the entity cannot further be divided and therefore forms a basal unit of taxonomy (Cracraft, 1987), with subspecies used as recognisable cryptic forms of a species complex and not basal taxonomic units in themselves (Maxwell & Dekkers, 2019). Finally, the species must offer a level of recognisable comparability to allow for systematic evaluation and the discernment of evolutionary history (Cracraft, 1987). The individualisation of a species can be problematic, particularly at the boundaries where the descriptive essences chosen to create the definition stray from the kind, obscuring the recognisable compatibility needed to generate a phylogeny. However, taxonomic realism can be achieved only when the taxonomist rejects limiting the definition of species by adherence to dogma and accepts that nature does not differentiate itself by a single unique classificatory unit or set of definitions inherent to a particular species concept (Ruse, 1998). Therefore, species-as-taxon are individuals formed out of a class consisting of a population, reflecting the reality that species are a taxonomic concept and not a category (Wiley, 1980).

The need to adhere rigidly to a single concept, and the ideology that once a species has been defined it is immutable, can hinder the greater understanding of the natural world (Knapp, 2008; Lugadha et al., 2018). There is a long historical acceptance that no single concept best encapsulates the idea of species, and that there is a need to utilise the way that is optimised to achieve comprehensibility and usefulness for the species to which the applied concept gives rise (Groot, 1938). Therefore, the approach to defining a species and its operation must, as a priority, grant the wider community outside the realm of semantic taxonomy a greater understanding of nature (Cracraft, 1987). Each of the monist species concepts relies on a single universal level of evolutionary units, but each is fundamentally unable to account for the diversity between organisms (Mishler & Donaghue, 1982; Rosindell et al., 2010; Alitto et al., 2019). It is only with a broad pluralist approach to the idea of species as the collective individual that evolutionary relationships can be explained taxonomically (Matos-Marvı et al., 2019).

Dealing with subspecies is problematic, and this is reflected in the lack of reference to them in the

conceptual literature. This is in part a consequence of the definition given to these lower taxonomic ranks such as temporarily isolated populations that are arbitrarily delimited and fated to reticulate back within other lineages (Frost & Kluge, 1994). However, the problem arises when the taxonomist is faced with making a subjective decision on whether a population is an arbitrary subspecies or a distinctive allopatric population with a distinctive evolutionary trajectory (Frost & Kluge, 1994). This leads to the argument that subspecies are not objective concepts (Groves, 2012). Maxwell & Dekkers (2019) argue that subspecies should be restricted to cryptic species where there are no physically observable boundaries to distinguish between populations; and that where boundaries are observable, species rank is justified.

The elevation of subspecies to full species ranking and the redrawing of existing phylogenies have consequences for the allocation of great reputational capital. This has a direct impact on all fields of biology, particularly the highly politicised fields of ecology and conservation biology (Tan et al., 2008; Frankham et al., 2012; Hey et al., 2003). Therefore, the arguments on the treatment of subspecies are even more controversial than debates over any singular particular species concept, which is why it is so often omitted from species debates. Notwithstanding, species are terminal in nature; thus, a taxonomically defined organism is a species, as it has taxonomical importance irrespective of conception (Maxwell & Dekkers, 2019).

HISTORICAL SPECIES CONCEPTUAL OVERVIEW

The number of species concepts that are in current use is a reflection of the treatment of the level of subtle distinctive phrasing that authors apply to a preferred concept; and its conceptual refinement is reflective of the lumping and splitting debates over species themselves (Groves, 2012; Mayden, 1999). The major conceptual frameworks proposed to delineate a species are each subdivided *ad infinitum* by individual graduation and augmentation as taxonomists have sought theoretical ascendancy, and have been driven to find the one true universal species theory. Fundamentally, all historical species concepts fall into one of four categories:

- 1) morphological or phenetical (primarily ahistorical);
- 2) biological (attribute or mechanism);

- 3) historical (common descent as the primary delineating factor); and
- 4) genetic, where nature is viewed as continuous and not discrete (Wheeler, 2007).

Phenetist- or morphological-based species concepts are those in which physical characters are utilised to formulate the fundamental division or class that is used to generate a species. This is fundamentally a classical approach in which there is an innate essence that distinguishes the organism (Mayr, 1987). Phenetic methodologies can be divided into two schools: Typological or Linnaean Species Concepts; and Morphological or Diagnostic Species Concepts.

The biological methodologies all have, at their core, a determination of species based on fitness and inheritance. The argument may be couched in terms of current or future biological isolation, depending on the methodological approach taken, or the current selective benefits a cline may have to its current environment. However, a considerable failure of the biological species methodologies is the need for the redefining of many of the currently accepted species, lumping of reticulating populations, and the application of these concepts to asexual biota (Hausdorf, 2011). There are four principal schools of biological speciation: Biological or Mixological Species Concepts; Behavioural or Recognition Species Concepts; Ecological or Differential Fitness Species Concepts; and Geographical Species Concepts.

The historical species concepts are based on cladistic analyses. They use cladistic tree divisions and are grounded in cleavage in the lineage of an organism, which can be traced, providing a temporal aspect to the definition (Hennig, 1965; Kornet, 1993). Historical concepts can be divided into two approaches, one in which the continuity is the fundamental driver of differentiation; and the other in which the recognition of distinctness predominates. The distinctness of the species as individual in the historical context is conceptualised in fundamental ways such as morphologically differentiable, adaptively distinct, geologically isolated, or tokogenetically isolated (Mishler & Donoghue, 1982). However, even more fundamental is the decrement of species from a delimiting point of divergence; and whether the original species is said to continue or is extinguished in the divergence event (Miller, 2001). A secondary fundamental issue for all historical methodologies concerns the treatment of reticulation among organisms; this gives rise to many of the symptomatic issues concerning

biological concepts (Hausdorf, 2011). There are four primary schools of historical speciation: Evolutionary or Unified Species Concepts; Hennigian General Lineage Species Concepts; Historical Continuity or Purist Phylogenetic Species Concepts; Historical Tokogenesis Species Concepts; and Phylogenetic or Historical Semphoranthy Species Concepts.

Dissimilarity models have an ideology that species should be considered in terms of the smallest delineation, a mereological approach to the delineation of entities based on similarities contained within the DNA, that has given rise to a plethora of physically indistinguishable cryptic species that should be treated as subspecies (Baker and Bradley, 2006; Mishler & Donoghue, 1982; Stauffer-Olsen et al., 2019; Maxwell & Dekkers, 2019). Ahistorical species concepts seek to find processes of speciation that differentiate sets of organisms. Notwithstanding the approach made to the species concept, there is an underlying commonality (intrinsic essence) based on a shared analogy and parallel evolution that creates a fundamental natural kind, which is delineated and classifiable (Hull, 1987). There are four principal schools of speciation based on genetic dissimilarity: Structural Species Concepts; Genetic or Genic Species Concepts; Cohesion or Continuous Stochastic Block Model Species Concepts; and Genotypic or Functional Clustering Species Concepts.

THE COMPLEXITY OF DEMARCATION

One of the challenges facing taxonomists is the determination of the level of difference that is considered significant enough to warrant the demarcation of a species from its sister taxa (Adams, 1998; Schutze et al., 2017). The adherence to a particular species concept limits the potential for the naming of new species (de Meeûs et al., 2003; Schlick-Steiner et al., 2010; Pante et al., 2015). Key to the determination of what constitutes a species is the understanding of the evolutionary trajectory of an organism and the level of reticulation with sister taxa that they may undergo (Adams, 1998; de Queiroz, 2005). However, the determination of future evolutionary trajectories is fraught with the danger of speculation and is often undertaken with a level of subjective evidence of directional change based on comparative phylogeny (Adams, 1998). There is now almost universal consensus that, irrespective of the choice of species concept chosen by the taxonomist, it is the demarcation of a distinctive evolutionary trajectory that unifies all concepts (de Queiroz, 2007).

The construction of phylogeny and the determination of species are often based on the sampling of taxa from an existing preconceived pool of organisms. These pools are derived from taxonomic assumptions that are based on existing notions of what species exist, and characters are drawn from a checklist of that group (Barraclough & Nee, 2001). This invariably opens the process of phylogenetic reconstruction to be based in the existing taxonomy, and invariably leads to the confounding and completely arbitrary splitting-lumping conundrum (Barraclough & Nee, 2001). The taxonomist seeks out the patterns of recurrence in nature and then makes the internal judgement of the significance of that pattern (Hey, 2001). Whether species are lumped together, or the level of variation is significant to enable the distinguishing of separate entities, it is conducted at the subjective judgement of the taxonomist and the weighting given to differing characteristics they determine to be consequential (Casanova, 2013). The approach taken in the determination of consequential characteristics is often biased by the discipline or taxonomic group with which the taxonomist is working and their requirement for taxonomic indicators (Kunz, 2002; Frankham et al., 2012). This invariably leads to a set of conditions, or criteria, that are used to generate the concept that is applied in the species diagnosis, often to the exclusion of all other species concepts. If species are comprised of multiple populations that are spatio-temporally separated with individual destinies either to reticulate, speciate or go extinct, then it is clear that there is no one conceptualised force that explains all the potentialities of divergence. Consequently, no one single species concept is able to encapsulate the entirety of the collective essences of the amalgamated organism clade to meet the needs of the taxonomic masses (Haveman, 2013).

One major failing with a hypothetical species is that the historical clustering of organisms that can be well defined and used to generate the spatio-temporal point at which a species is delimited creates the problem of omitting transitional forms (Girard & Renaud, 2011). Similarly, populations may be heterospecific and may be part of more than one species by definition (González-Forero, 2009). Heterospecificity is one of the major problems when demarcating the boundaries of agamic groups and is a primary reason that most species concepts omit an argument on asexuality (Hausdorf, 2011; Haveman, 2013).

Discrete discernment of kinds, which are sound in their spatio-temporal position and are not singularly

based upon particular apomorphs, will give rise to the collective individual and offer basal soundness to any clade (Baum & Donoghue, 1995; de Queiroz & Gauthier, 1994). The monist argument that pluralism leads to confusion through a lack of intrinsic meaning in the term 'species' can be overcome when the taxonomist is explicit in the method and conceptionality (Schlick-Steiner et al., 2010). The use of essentialistic pluralism delineates a set of organisms from the natural world at a particular spatio-temporal point and that contains enough meaning to enable discrimination and thus allow for an organism's taxonomic discernment. It is the failing of hierarchical taxonomic theory that, even if kinds are well defined, there remains a distinct lack of evolutionary theory in the relationships between higher taxa.

REVIEWING PLURALISM

The essentialistic pluralist approach does not seek to tie the taxonomist down to one species concept, but rather enables a choice in definition to be applied based on the uniqueness of the characteristics of the organism as a set, and thus is an extension of the reality that taxa are entities that currently exist, or have existed, within a temporal space and are in need of demarcation and explanation (Kitcher, 1984, 1984a). This is the theoretical underpinning for integrative taxonomic practice with its universality in choice of criteria with maximum defensibility of demarcation (Yeates et al., 2011; Schutze et al., 2017), but further adds a spatio-temporal constraint. This temporalism must still include innate references to the organisms that are historically related, as the removal of the historical context itself reduces the meaning of species and is a major cause of inconsistency, even in the face of disconnectivity of lineages (Ereshefsky, 1992). Ereshefsky (1992) noted that pluralistic species concepts allow for the coverage of the multiplicity of evolutionary forces that drive divergences, such as interbreeding, selection, genetic homeostasis, common descent, and developmental and ecological isolation: this conceptual approach formed the basis for integrated taxonomy (Schlick-Steiner et al., 2010; Pante et al., 2015; Solari et al., 2019). This reflects the reality of the natural world. Mayr (1987, p. 149) argues that the pluralist approach failed through the inability to distinguish the species category and the species organism: "mammals, hairy caterpillars, hairy seeds of certain plants and other hairy objects, would make a legitimate set" and therefore a heterogeneous species. Mayr (1987) fails to recognise that pluralist species are

discrete individuals, a collective set bounded in time, having a real meaning used to describe the observable and not categorical abstractions. True pluralism needs to be free from any structural boundaries and overcomes the underlying complexities of the species argument to enable a taxonomist to enunciate a greater accuracy in the phylogenetic classificatory process. This is achieved through the enabling of individuality through the recognition of set complexity (Lombard et al., 2010).

Mishler & Donoghue (1982) argue that species should not be separated from higher ranks, but form a natural extension of them; and should be viewed as assemblages united by descent, not as individuals. However, the acceptance of individuality enables the taxonomist to draw a spatiotemporal line as to the kinds that are to be used in classification. These kinds then enable the understanding of higher ranks based on evolutionary relationships. Not accepting species as individuals means that the basis of higher taxonomy is grounded in arbitrariness and thus rendered meaningless. The term ‘exclusivity’ can be associated with kinds and is the foundation of the coalescence theory, that biological entities are closely related to a particular group and thus objectively discernible (Baum & Donoghue, 1995).

Mayden (1999) conceived the consistent approach of species delimitation, in which there was an encouragement of cooperation in the understanding of diversity and for conceptual monism. At the heart of this monist approach is the recognition of the species based on a description or diagnosis that is used as the criterion for demarcation, which is then defined by a concept (Mayden, 1999). However, one universal failure of species concepts is the lack of conceptual definition, which should be resolved before the population can be determined (Hausdorf, 2011). This is probably more relevant to species delineation than any conceptual approach. Hey (2006, p. 459) argued that “detection protocols are not concepts” and the taxonomist needs to separate the criteria for delineating species from the “theoretical understanding of the way species exist”, that is, the concept. This idea places the recognition of a species outside the confines of any preconception of how a species should be conceptualised. There is a need for species pluralism, which is the overarching monist concept, and has been the underlying goal of all species conceptual arguments.

A fundamental pluralistic approach seeks to bring an overarching conceptuality to the differing species

concepts in which the goal was not an abandonment of any one concept *per se*, but rather an acceptance that each concept is an operational tool to be used in the discovery of the species (Mayden, 1999). The determination of the evolutionary trajectory has priority in species demarcation, and the species concept applied is merely the tool to enable recognition of that evolutionary event at a point in time.

One of the major issues that distinguishes species concepts is the determination of whether the process of evolutionary separation has been finalised, or is an on-going process marked with a lack of complete biological separation of the populations. There is a growing shift to accept species as evolutionary populations and a realisation that criteria for delimiting these species cannot be restricted, but rather need to be based on factors that are outside the confines of any one isolating biological property (Naomi, 2011). That is, under essentialist pluralism, the taxonomist may be aware of an essential characteristic that makes a species unusual and distinctive. This then forms the basis for a criterion, and integrated taxonomy allows the taxonomist to be free to determine a conceptual approach that provides the framework for naming a new taxon based on that distinctiveness. Therefore, under essentialist pluralism, there is no restriction on which concept is used to delineate an organism. However, there is a need to restrict the species to a point in time with a defined morphospace. Thus, this conceptual freedom demands that taxonomists accept an obligation to be true to the phylogeny and thus must justify the choice of species concept, both in terms of a criterion for distinction, as well as offering an explanation for the cause of that species’ existence, as well as stating its relationships with others placing the organism in context.

PHILOSOPHICAL FAILINGS

Many of the reviews of species concepts fail to explore essentialist arguments, or when this exploration is carried out, it is with the basic premise that all essentialist arguments are phenetic. However, one of the major failings of the current essentialist approach to species criteria is the decision that species concepts are facts and, therefore, acceptable to be used taxonomically (Hey, 2006). This clearly is the crux of the problem. Taxonomists fail to recognise that species have two parts: the criteria with the distinctive hypothetical process of species delimitation with the rigidity to a concept; and the conception itself, which is hypothetical (Paul, 2002). The natural consequence

of failing to recognise these two parts explains why the treatment of complex taxonomic clusters, such as agamics, is overlooked in conceptual formulations. It is only with integrated taxonomy that the taxonomist is freed from the theoretical constraints of taxonomic rigidity imposed by doctrinal adherence to a single hypothetical species concept and is able to explore the criteria of the real organism necessary to impart taxonomic meaning (Schlick-Steiner et al., 2010). Essentialistic pluralism, through the use of integrated taxonomic practice, provides an explicit spatio-temporal point necessary to impart taxonomic meaning; and therefore, provide reference points for evolutionary contextualisation as an organism morphs through time.

Fundamentally, species need to be conceptualised outside of taxonomic classificatory systems as they fall outside of systematic hierarchical arguments (Dubois, 2011). Thus, the use of subspecies is arbitrary, with all-natural entities worthy of species consideration if they are observably distinguishable, even if this is only spatially significant (Maxwell & Dekkers, 2019). This is because species, although hypothetically chosen, remain real entities, represented by collective individual populations and not just intentional meanings derived by the taxonomist, which is inherently what higher classifications are (Ghiselin, 1974; Hull, 1976). This raises a point of contention: if species are real, why are many of the concepts that are used to define them based on unreal or non-causal criteria? This leads to a complexity in conceptual realisation and invariably to conceptual misunderstanding, a problem absent in higher taxonomic arguments that have no physical reality or place in species debates (Stamos, 2003).

IMPLICATIONS FOR DISCERNING SPECIES

Recent evolutionary essentialism has, at its core, a sense of indeterminacy in the definition of what constitutes a species (Devitt, 2010). This indeterminacy can be countered if a species is first viewed as an individually unified population representing hypotheses that explain the convergence of both intrinsic and extrinsic structural essences. The acceptance of essences as having intrinsic and extrinsic properties highlights one of the theoretical failings of the current anti-essentialism debate, where species are delineated primarily on intrinsically pseudo-phenetically inclined parameters (Lewens, 2012). The intrinsic and extrinsic structural essences of collective higher taxa particular to a clade are used to form a continuum, the essence matrix,

from which the organism state is then delineated. This organism state represents a static cross-section in the evolutionary history of a real population that contains all the phylogenetically restricted character essences that are exhibited by the organism and allows for group delineation (Pleijel & Rouse, 2000; Figure 2).

The evolutionary progression of the organism is phylogenetically constrained by the evolving and limiting structural essences. This idea of structural essences forming a unified entity is in the true Aristotelian tradition (Dumsday, 2012). Notwithstanding, the concept of phylogeny generated by the new evolutionary synthesis necessitates that these structural essences are viewed as spatio-temporally mutable. Therefore, structural essences are to be seen as historical and, possibly, variably pluralistic in nature, and in turn they reference the wider immutable spatio-temporal.

CONCLUSION

The reliance on species relational concepts without an evolutionary context, and the linking of phenetic ideology with the concept of essence, is a failing in much of current essentialist and anti-essentialist arguments (Lewens, 2012). It is only the understanding of the structural essence itself, with knowledge of the driving forces and processes that gave rise to that essence, which enables the discernment of analogies and reveals the true phylogenesis of an organism. It is how the cladist or taxonomist deals with the delineation of stages in the evolutionary progression of structural essences that then forms the basis of the restriction of the organism state and how the kind is defined. This is then consequently reflected in the criteria used in the choice of model of speciation and conception that is utilised to impart taxonomic meaning to all hypothetical entities called a species.

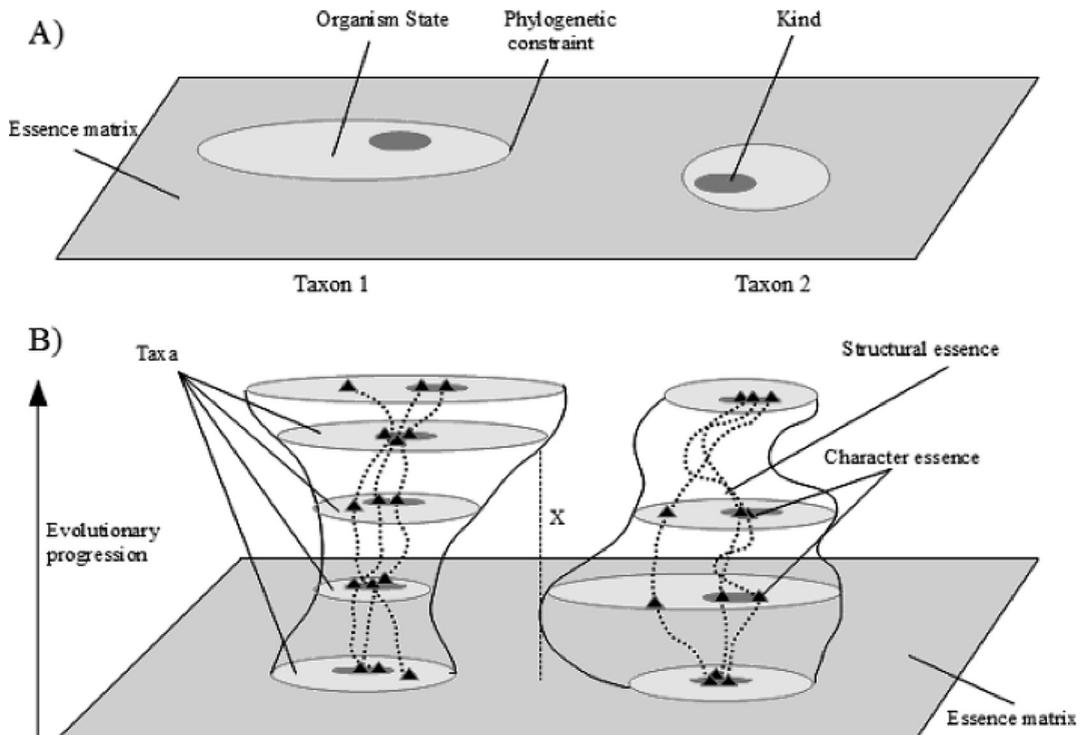
Once the taxonomist has distinguished the evolutionary trajectory of an organism based on any criterion, there is freedom to determine an appropriate conceptual approach to justify the recognition of the new species. The only requirement that is placed on the taxonomist is the need for explicitness in the justification for that conceptual choice. Essentialistic pluralism generates hypothetical terminal taxonomic units from which phylogenies are then constructed. Therefore, delimitation of species has a critical impact on the understanding of evolutionary biology where they form the spatio-temporal kind within an essence matrix, the continuum of evolutionary descent. The use of essentialistic pluralism, with its unrestricted

approach to conceptualisation of what is a species, using integrated taxonomy with spatio-temporal limitations, allows the taxonomist the freedom to express a unique approach to exploring phylogeny without the shackles of rigid necessity to declare adherence to a single species concept. Essentialist pluralism is, therefore, the gold standard for universality and is the conceptual monist Holy Grail that has underpinned the rhetoric of species debates for centuries. It is only the fear of loss of reputational capital by taxonomists who have spent their lives arguing for one concept that implicitly holds integrated taxonomy back from achieving universal acceptance.

The conceptual monist argument that pluralism leads to confusion through a lack of intrinsic meaning in the term 'species' can be overcome when the taxonomist is explicit. The use of essentialist pluralism delineates a set of organisms from the natural world

that contains enough meaning to enable discrimination and thus allow for an organism's taxonomic discernment. It is the failing of hierarchical taxonomic theory that, even if kinds are well defined, there remains a distinct lack of evolutionary theory or the concept that the describing author had for the relationships between higher taxa. Therefore, essentialistic pluralism addresses the issue of species demarcation at its core. Once the taxonomist has distinguished the evolutionary trajectory of an organism based on any criterion, there is freedom to determine an appropriate conceptual approach to justify the recognition of the new species. The only requirement that is placed on the taxonomist is the need for explicitness in the justification for that conceptual choice. This invariably makes sub-specific ranks taxonomically meaningless, and invariably recognises all ranks below species as individual evolutionary lines worthy of full species

FIGURE 2. The two fundamental essentialist ideologies: A) the phenetic approach, which does not include evolutionary progression; and B) the essential pluralist approach, in which structural essences are used to delineate an organism state with character essences in temporal stasiogenesis within the evolutionary continuum. Organisms may show similar structural essences (X) as a consequence of occupying the same position within the essence matrix, this may arise from a mechanism such as convergence. Each of the taxa that overlaps can be readily distinguished from the other through an understanding of their evolutionary progression. The essence matrix is the the evolutionary potential of an organism that confines the character limits.



recognition. That is, subspecies should be used for cryptic species and the examination of clinal variations (Maxwell & Dekkers, 2019). This leads to an argument for the use of monomial terminal taxonomy. Further, this new taxonomic approach to species conceptualisation has significant implications for the assignment of higher taxonomy, which is often more a reflection of the lack of ‘room’ at the lower cladistic levels under the draconian Linnaean rigid methodology which is being challenged with the introduction of phylogenetic nomenclature under the PhyloCode. Essentialistic pluralism and terminal taxonomy present a new approach to species and are natural extensions of using rank-free phylogenetic taxonomy in higher classification with spatio-temporal restrictions.

The Linnaean system is a set of informal hierarchies that simply groups organisms into clusters based on taxonomic preference, which are then named relative to each other without the need for historical consideration of any higher relationship. This lack of relational meaning can be traced back to the fact that relational understanding of higher systematics fundamentally eluded Linné. The need to explain evolutionary trends has become an important facet in the modern evolutionary synthesis, and such evolutionary processes and patterns need to be reflected in the nomenclature. This contextual ambiguity has left Linnaean taxonomy

struggling to demonstrate true historical relationships between the taxa within clades. Therefore, there is a strategic need to revise the lower order taxonomy and in particular revisit the idea of uninomials to avoid arbitrary cladistics rankings.

Essentialistic pluralism addresses the issue of species demarcation at its core. Once the taxonomist has distinguished the evolutionary trajectory of an organism based on any criterion, there is freedom to determine an appropriate conceptual approach to justify the recognition of the new species. The only requirement that is placed on the taxonomist is the need for explicitness in the justification for that conceptual choice. This invariably makes sub-specific ranks taxonomically meaningless and recognises all ranks below species as individual evolutionary lines worthy of full species recognition. This leads to an argument for the use of terminal taxonomy to be declared to anchor all levels of nomenclature. Further, this new taxonomic approach to species conceptualisation has significant implications for the assignment of higher taxonomy, which is often more a reflection of the lack of ‘room’ at the lower cladistic levels under the draconian Linnaean rigid methodology. Essentialistic pluralism and terminal taxonomy combined present a new approach to species, and this is a natural consequence of using rank-free phylogenetic taxonomy in higher classification.

LITERATURE CITED

- Adams, B. J. (1998). Species concepts and the evolutionary paradigm in modern nematology. *Journal of Nematology*, 31(1), 1–21.
- Alitto, R. A.d.S., Amaral, A. C. Z., de Olivera, L. D., Serrano, H., Seger, K. R., Damian, P., Guilherme, B., Di Domenico, M., Christensen, A. B., Lourenço, L. B., Tavares, M., & Borges, M. (2019). Atlantic west *Ophiothrix* spp. in the scope of integrative taxonomy: confirming the existence of *Ophiothrix trinidadensis* Tommasi, 1970. *PLoS ONE*, 14(1), e0210331.
- Amundson, R. (1998). Typology reconsidered: two doctrines on the history of evolutionary biology. *Biology and Philosophy*, 13, 153–177.
- Andersson, L. (1990). The driving force; species concepts and ecology. *Taxon*, 39(3), 375–382.
- Avise, J. C., Arnold, J., Ball, R. M., Berminham, E., Lamb, T., Neigel, J. E., Reeb, C. A., & Saunders, N. (1987). Intraspecific phylogeography: the mitochondrial DNA bridge between population genetics and systematics. *Annual Review of Ecology and Systematics*, 18, 489–522.
- Aze, T., Ezard, T. H. G., Purvis, A., Coxall, H. K., Stewart, D. R. M., Wade, B. S., & Pearson, P. N. (2013). Identifying anagenesis and cladogenesis in the fossil record. *Proceedings of the National Academy of Sciences*, 110(13), E2946.
- Baker, R. J., & Bradley, R. D. (2006). Speciation in mammals and the generic species concept. *Journal of Mammalogy*, 87(4), 643–662.
- Barracough, T. G., & Nee, S. (2001). Phylogenetics and speciation. *Trends in Ecology and Evolution*, 16(7), 391–399.
- Baum, D. A., & Donoghue, M. J. (1995). Choosing among Alternative “Phylogenetic” species concepts. *Systematic Botany*, 20(4), 560–573.

- Brady, R. H. (1982). Theoretical issues and “Pattern Cladistics”. *Systematic Zoology*, 31(3), 286–291.
- Bremer, K., & Wanntorp, H.-E. (1979). Geographic populations or biological species in phylogeny reconstruction. *Systematic Zoology*, 28(2), 220–224.
- Brummitt, R. K. (2002). How to chop up a tree. *Taxon*, 51, 31–41.
- Brundin, L. (1972). Evolution, causal biology, and classification. *Zoologica Scripta*, 1(3–4), 107–120.
- Bryant, H. N. (1996). Explicitness, stability, and universality in the phylogenetic definition and usage of taxon names: a case study of the phylogenetic taxonomy of the Carnivora (Mammalia). *Systematic Biology*, 45(2), 174–189.
- Cantino, P. D., Bryant, H. N., De Queiroz, K., Donoghue, M. J., Eriksson, T., Hillis, D. M., & Lee, M. S. Y. (1999). Species names in phylogenetic nomenclature. *Systematic Biology*, 48(4), 790–870.
- Casanova, M. T. (2013). Review of the species concepts *Chara fibrosa* and *C. flaccida* (Characeae, Charophyceae). *Australian Systematic Botany*, 26, 291–297.
- Chambers, G. (2012). The species problem: seeking new solutions for philosophers and biologists. *Biological Philosophy*, 27, 755–765.
- Cracraft, J. (1987). Species concepts and the ontology of evolution. *Biology and Philosophy*, 2, 329–346.
- Crusafont-Pairó, M., & Truyols-Santonja, J. (1958). A quantitative study of stasigenesis in fissiped carnivores. *Nature*, 181(4604), 289–290.
- Darwin, C. (1859). *On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life*. John Murray.
- de Meeûs, T., Durand, P., & Renaud, F. (2003). Species concepts: what for? *Trends in Parasitology*, 19(10), 425–427.
- de Pinna, M. C. C. (1991). Concepts and tests of homology in the cladistic paradigm. *Cladistics*, 7, 367–394.
- de Pinna, M. C. C. (1999). Species concepts and phylogenetics. *Reviews in Fish Biology and Fisheries*, 9, 353–373.
- de Queiroz, K. (2005). Different species problems and their resolution. *BioEssays*, 27, 1263–1269.
- de Queiroz, K. (2007). Species concepts and species delimitation. *Systematic Biology*, 56(6), 879–886.
- de Queiroz, K., & Gauthier, J. (1994). Towards a phylogenetic system of biological nomenclature. *TREE*, 9(1), 27–31.
- Devitt, M. (2008). Resurrecting biological essentialism. *Philosophy of Science*, 75(3), 344–382.
- Devitt, M. (2010). Species have (partly) intrinsic essences. *Philosophy of Science*, 77(5), 648–661.
- Dobzhansky, T. (1935). A critique of the species concept in biology. *Philosophy of Science*, 2, 344–355.
- Dobzhansky, T. (1951). *Genetics and the Origin of Species* (3rd ed.). Columbia University Press.
- Dubois, A. (2011). Species and “strange species” in zoology: Do we need a “unified concept of species”? *Comptes Rendus Palevol*, 10, 77–94.
- Dumsday, T. (2012). A new argument for intrinsic biological essentialism. *The Philosophical Quarterly*, 62(248), 486–504.
- Dupré, J. (1981). Natural kinds and biological taxa. *The Philosophical Review*, 90(1), 66–90.
- Elder, C. L. (2008). Biological species are natural kinds. *Southern Journal of Philosophy*, 46, 339–362.
- Ereshefsky, M. (1992). Eliminative pluralism. *Philosophy of Science*, 59(4), 671–690.
- Forey, P. L. (2002). PhyloCode – pain, no gain. *Taxon*, 51(1), 43–54.
- Frankham, R., Ballou, J. D., Dudash, M. R., Eldridge, M. D. B., Fenster, C. B., Lacy, R. C., Mendelson III, J. R., Porton, I. J., Ralls, K., & Ryder, O. A. (2012). Implications of different species concepts for conserving biodiversity. *Biological Conservation*, 153, 25–31.
- Frost, D. R., & Kluge, A. G. (1994). A consideration of epistemology in systematic biology, with special reference to species. *Cladistics*, 10, 259–294.
- Gangloff, M. M. (2019). Editorial: The importance of integrated taxonomy to freshwater conservation. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 29, 521–527.
- Garnett, S. T., & Christidis, L. (2017). Taxonomy anarchy hampers conservation. *Nature*, 546, 25–27.
- Ghiselin, M. T. (1974). A radical solution to the species problem. *Systematic Zoology*, 23(4), 536–544.
- Girard, C., & Renaud, S. (2011). The species concept in a long-extinct fossil group, the conodonts. *Comptes Rendus Palevol*, 10, 107–115.

- González-Forero, M. (2009). Removing ambiguity from the biological species concept. *Journal of Theoretical Biology*, 256, 76–80.
- Gould, S. J. (1977). *Ontology and Phylogeny*. Harvard University Press.
- Grout, A. J. (1938). The species concept. *The Bryologist*, 41(3), 49–50.
- Groves, C. (2012). Species concepts in primates. *American Journal of Primatology*, 74, 687–691.
- Hausdorf, B. (2011). Progress toward a general species concept. *Evolution*, 65(4), 923–931.
- Haveman, R. (2013). Freakish patterns – species and species concepts in apomicts. *Nordic Journal of Botany*, 31, 257–269.
- Hennig, W. (1965). Phylogenetic Systematics. *Annual Review of Entomology*, 10, 97–116.
- Henry, D. (2011). Aristotle's pluralistic realism. *The Monist*, 94(2), 197–220.
- Hey, J. (2001). The mind of the species problem. *Trends in Ecology and Evolution*, 16(7), 326–329.
- Hey, J. (2006). On the failure of modern species concepts. *Trends in Ecology and Evolution*, 21(8), 447–450.
- Hey, J., Waples, R. S., Arnold, M. L., Butlin, R. K., & Harrison, R. G. (2003). Understanding and confronting species uncertainty in biology and conservation. *Trends in Ecology and Evolution*, 18, 597–603.
- Hull, D. L. (1976). Are species really individuals? *Systematic Zoology*, 25(2), 174–191.
- Hull, D. L. (1980). Individuality and Selection. *Annual Review of Ecology and Systematics*, 11, 311–332.
- Hull, D. L. (1987). Genealogical actors in ecological roles. *Biology and Philosophy*, 2, 168–184.
- Huxley, J. (1957). The three types of evolutionary process. *Nature*, 180(4584), 454–455.
- Kitcher, P. (1981). Explanatory unification. *Philosophy of Science*, 48(4), 507–531.
- Kitcher, P. (1984). Species. *Philosophy of Science*, 51(2), 308–333.
- Kitcher, P. (1984a). Against the monism of the moment: a reply to Elliott Sober. *Philosophy of Science*, 51(4), 616–630.
- Kitts, D. B., & Kitts, D. J. (1979). Biological Species are natural kinds. *Philosophy of Science*, 46, 613–22.
- Knapp, S. (2008). A century of evolution: Ernst Mayr (1904–2004), species concepts and floras: what are species for? *Biological Journal of the Linnean Society*, 95, 17–25.
- Kornet, D. J. (1993). Permanent splits as speciation events; a formal reconstruction of the internodal species concept. *Journal of Theoretical Biology*, 164, 407–435.
- Kunz, W. (2002). Species concepts versus species criteria. *Trends in Parasitology*, 18(10), 440.
- Lamarck, J.-B. (1801). *Système des animaux sans vertèbres*. J.-B. Lamarck.
- Lewens, T. (2012). Species, essence and explanation. *Studies in History and Philosophy of Biological and Biomedical Science*, 43, 751–757.
- Lewis, J. E. (1963). A short history of taxonomy from Aristotle to Linnaeus. *Medical Arts and Sciences*, 17, 106–123.
- Lombard, L., Crous, P. W., Wingfield, B. D., & Wingfield, M. J. (2010). Species concepts in *Calonectria* (*Cylindrocladium*). *Studies in Mycology*, 66, 1–14.
- Losos, J. B., & Glor, R. E. (2003). Phylogenetic comparative methods and the geography of speciation. *Trends in Ecology and Evolution*, 18(5), 220–227.
- Lughadha, E. M. N., Staggenieier, V. G., Vasconcelos, T. N. C., Walker, B. E., Canteiro, C., & Lucas, E. J. (2018). Harnessing the potential of integrated systematics for conservation of taxonomically complex, megadiverse plant groups. *Conservation Biology*, 3(3) 511–522.
- Matos-Maraví, P., Wahlberg, N., Antonelli, A., & Penz, C. M. (2019). Species limits in butterflies (Lepidoptera: Nymphalidae): reconciling classical taxonomy and with the multispecies coalescent. *Systematic Entomology*, 44, 745–756.
- Maxwell, S. J., & Dekkers, A. M. (2019). A new name for *Altivasum typicum* Hedley, 1916 fide Dekkers and Maxwell, 2018 and the description of *Altivasum clarksoni* n. sp. *The Festivus*, 51(2), 171–176.
- Mayden, R. L. (1999). Consilience and a hierarchy of species concepts: advances toward closure on the species puzzle. *Journal of Nematology*, 31(2), 95–116.
- Mayr, E. (1987). Ontological status of species: scientific progress and philosophical terminology. *Biology and Philosophy*, 2, 145–166.
- Mayr, E. (1996). What is a species, and what is not? *Philosophy of Science*, 63(2), 262–277.

- Miller, W. (2001). The structure of species, outcomes of speciation and the 'species problem': ideas for paleobiology. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 176, 1–10.
- Mishler, B. D., & Donoghue, M. J. (1982). Species concepts: A case for pluralism. *Systematic Zoology*, 31(4), 491–503.
- Moritz, J. M. (2013). God's creation through evolution and the language of scripture. *Theology and Science*, 11(1), 1–7.
- Nadachowski, A. (1993). The species concept and quaternary mammals. *Quaternary International*, 19, 9–11.
- Naomi, S.-I. (2011). On the integrated frameworks of species concepts: Mayden's hierarchy of species concepts and de Queiroz's unified concept of species. *Journal of Zoological Systematics and Evolutionary Research*, 49(3), 177–184.
- Nixon, K. C., & Wheeler, Q. D. (1990). An amplification of the phylogenetic species concept. *Cladistics*, 6, 211–223.
- Noor, M. A. F. (2002). Is the biological species concept showing its age? *Trends in Ecology and Evolution*, 17(4), 153–154.
- Oderberg, D. (2007). *Real Essentialism*. Routledge.
- Okasha, S. (2002). Darwinian metaphysics: species and the question of essentialism. *Synthese*, 131(2), 191–213.
- Pante, E., Schoelinc, C., & Puillandre, N. (2015). From integrative taxonomy to species description; one step beyond. *Systematic Biology*, 64(1), 152–160.
- Pardo-Díaz, C., Toro, A. L., Tovar, S. A. P., Sarmiento-Garcés, R., Herrera, M. S., & Salazar, C. (2019). Taxonomic reassessment of the genus *Dichotomius* (Coleoptera: Scarabaeinae) through integrative taxonomy. *PeerJ*, 7, e7332.
- Paul, R. (2002). Species concepts versus species criteria. *Trends in Parasitology*, 18(10), 439–440.
- Pavan, A. C., & Marroig, G. (2016). Integrating multiple evidences in taxonomy; species diversity and phylogeny of mustached bats (Mormoopidae: *Pteronotus*). *Molecular Phylogenetics and Evolution*, 103, 184–198.
- Pleijel, F., & Rouse, G. W. (2000). Least-inclusive taxonomic unit: a new taxonomic concept for biology. *Proceedings of the Royal Society of London*, 267, 627–630.
- Rosindell, J., Cornell, S. J., Hubbell, S. P., & Etienne, R. S. (2010). Protracted speciation revitalizes the neutral theory of biodiversity. *Ecological Letters*, 13, 716–727.
- Ruse, M. (1998). All my love is towards individuals. *Evolution*, 52(1), 283–288.
- Schlick-Steiner, B. C., Steiner, F. M., Seifert, B., Stauffer C., Christian, E., & Crozier, R. H. (2010). Integrative Taxonomy: A multisource approach to exploring biodiversity. *The Annual Review of Entomology*, 55, 421–438.
- Schutze, M. K., Virgilio, M., Norrbom, A., & Clarke, A. R. (2017). Tephritid integrative taxonomy: Where we are now, with a focus on the resolution of three tropical fruit fly species complexes. *Annual Review of Entomology*, 62, 147–164.
- Solari, S., Stoeri-Caio, C. G., & Baker, R. J. (2019). Advances in systematics of bats: towards a consensus on species delimitation and classification through integrative taxonomy. *Journal of Mammalogy*, 100(3), 838–851.
- Stamos, D. N. (2003). *The Species Problem: Biological Species, Ontology, and the Metaphysics of Biology*. Lexington Books.
- Stauffer-Olsen, N. J., O'Grady, P. M., & Resh, V. H. (2019). Cytochrome oxidase I sequences from northern and southern California suggest cryptic *Baetis* (Ephemeroptera: Baetidae) species. *Western North American Naturalist*, 79(2), 204–218.
- Szalay, F. S., & Bock, W. J. (1991). Evolutionary theory and systematics: relationships between process and patterns. *Zoological Systematics and Evolutionary Research*, 29, 1–39.
- Tan, D., Ali, F., Kutty, S. N., & Meier, R. (2008). The need for specifying species concepts: How many species of silvered langurs (*Trachypithecus cristatus* group) should be recognized? *Molecular Phylogenetics and Evolution*, 49, 688–689.
- Thomson, S. A., Pyle, R.L., Ahyong, S. T., Alonso-Zarazaga M., Ammirati, J., Araya, J. F., Ascher, J. S., Audisio, T. L., Azevedo-Santos, V. M., Bailly, M., Baker, W. J., Balke, M., Barclay, M. V. L., Barrett, R. L., Benine, R. C., Bickstaff, J. R. M., Bouchard, P., Bour, R., Bourgoin, T., Boyko, C. B., Abraham S. H., Breure, A. S. H.,

- Brothers, D. J., Byng, J. W., Campbell, D., Cerfaco, L. M. P., Cernák, I., Cerretti, P., Chang, C.-H., Cho, S., Copus, J. M., Costello, M. J., Cseh, A., Csuzdi, C., Culham, A., D'Elia, G., d'Udekem d'Acoz, C., Daneliya, M. E., Dekker, R., Dickinson, E. C., Dickinson, T. A., van Dijk, P. P., Dijkstra, K.-D. B., Dima, B., Dmitriev, D. A., Duistermaat, L., Dumbacher, J. P., Eiserhardt, W. L., Ekrem, T., Evenhuis, N. L., Faille, A., Fernández-Triana, J. L., Fiesler, E., Fishbein, M., Fordham, B. G., Freitas, A. V. L., Friol, N. R., Fritz, U., Frøslev, T., Funk, V. A., Gaimari, S. D., Garbino, G. S. T., Garraffoni, A. R. S., Geml, J., Gill, A. C., Gray, A., Graziotin, F. G., Greenslade, P., Gutiérrez, E. E., Harvey, M. S., Hazevoet, C. J., He, K., He, X., Helfer, S., Helgen, H. M., van Heteren, A. H., Hita Garcia, F., Holstein, N., Horváth, M. K., Hovenkamp, P. H., Hwang, W. S., Hyvönen, J., Islam, M. B., Iverson, J. B., Ivie, M. A., Jaafar, Z., Jackson, M. D., Jayat, J. P., Johnson, N. F., Kaiser, H., Klitgård, B. B., Knapp, D. G., Kojima, J., Kõljalg, U., Kontschán, J., Krell, F.-T., Krisai-Greilhuber, I., Kullander, S., Latella, L., Lattke, J. E., Lencioni, V., Lewis, G. P., Lhano, M. G., Lujan, N. K., Luksenburg, J. A., Mariaux, J., Marinho-Filho, J., Marshall, C. J., Mate, J. F., McDonough, M. M., Ellinor Michel, E., Miranda, V. F. O., Mitroiu, M.-D., Molinari, J., Monks, S., Moore, A. J., Moratelli, R., Murányi, D., Nakano, T., Nikolaeva, S., Noyes, J., Ohl, M., Oleas, N. H., Orrell, T., Páll-Gergely, B., Pape, T., Papp, V., Parenti, L. R., Patterson, D., Pavlinov, I. Y., Pine, R. H., Poczai, P., Prado, J., Prathapan, D., Richard, K., Rabeler, R. K., Randall, J. E., Rheindt, F. E., Rhodin, A. G. J., Rodríguez, S. M., Rogers, D. C., Roque, F. de O., Rowe, K. C., Ruedas, L. A., Salazar-Bravo, J., Salvador, R. B., Sangster, G., Sarmiento, C. E., Schigel, D. S., Schmidt, S., Schueler, F. W., Segers, H., Snow, N., Souza-Dias, P. G. B., Stals, R., Stenroos, S., Stone, R. D., Sturm, C. F., Štys, P., Teta, P., Thomas, D. C., Timm, R. M., Tindall, B. J., Todd, J. A., Triebel, D., Valdecasas, A. G., Vizzini, A., Vorontsova, M. S., Vos, J. M. de, Wagner, P., Watling, L., Weakley, W., Welter-Schultes, F., Whitmore, D., Wilding, N., Will, K., Williams, J., Wilson, K., Winston, J. E., Wüster, W., Yanega, D., Yeates, Y., Zaher, Z., Zhang, G., Zhang, Z.Q., & Zhou, H. Z. (2018, March). Taxonomy based on science is necessary for global conservation. *PLoS Biology*, *16*(3), e2005075.
- Wallace, S. (2002). In defence of biological essentialism. *Philosophia Christi*, *4*, 29–43.
- Walsh, D. (2006). Evolutionary essentialism. *British Journal for the Philosophy of Science*, *57*, 425–448.
- Wheeler, Q. D. (2007). Invertebrate systematics or spineless taxonomy? *Zootaxa*, *1668*, 11–18.
- Wiley, E. O. (1980). Is the evolutionary species fiction? – A consideration of classes, individuals and historical entities. *Systematic Zoology*, *29*(1), 76–80.
- Winsor, M. P. (2006). Linnaeus's biology was not essentialist. *Annals of the Missouri Botanical Garden*, *93*(1), 2–7.
- Wright, S. (1932). The Roles of Mutation, Inbreeding, Crossbreeding, and Selection in Evolution. *Proceedings of the Sixth International Congress of Genetics*, *1*, 356–366.
- Yeates, D. K., Seago, A., Nelson, L., Cameron, S. L., Joseph, L., & Trueman, J. W. H. (2011). Integrative taxonomy, or iterative taxonomy? *Systematic Entomology*, *36*, 209–217.

AUTHOR PROFILE

Stephen Maxwell is a doctoral candidate at James Cook University researching radiation and reticulation of gastropods during the recent interglacial cycles. He has a keen interest in the philosophy of science in relation to speciation theory, with a goal of uniting nomenclature and phylogenetics. Prior to undertaking studies in the sciences, he studied history and classics and has a passion for archaic Greek poetry.