



## REVIEW

# Lineages, splits and divergence challenge whether the terms anagenesis and cladogenesis are necessary

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Using the framework of evolutionary lineages to separate the process of evolution and classification of species, we observe that ‘anagenesis’ and ‘cladogenesis’ are unnecessary terms. The terms have changed significantly in meaning over time, and current usage is inconsistent and vague across many different disciplines. The most popular definition of cladogenesis is the splitting of evolutionary lineages (cessation of gene flow), whereas anagenesis is evolutionary change between splits. Cladogenesis (and lineage-splitting) is also regularly made synonymous with speciation. This definition is misleading as lineage-splitting is prolific during evolution and because palaeontological studies provide no direct estimate of gene flow. The terms also fail to incorporate speciation without being arbitrary or relative, and the focus upon lineage-splitting ignores the importance of divergence, hybridization, extinction and informative value (i.e. what is helpful to describe as a taxon) for species classification. We conclude and demonstrate that evolution and species diversity can be considered with greater clarity using simpler, more transparent terms than anagenesis and cladogenesis. Describing evolution and taxonomic classification can be straightforward, and there is no need to ‘make words mean so many different things’. © 2015 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2016, **117**, 165–176.

**ADDITIONAL KEYWORDS:** anagenetic – cladogenetic – evolutionary lineage – macroevolution – microevolution – paleontology – phylogenetics – speciation – species – splitting.

### THE EVOLUTIONARY PROCESS AND SPECIATION

In this review, we assess the terms ‘anagenesis’ and ‘cladogenesis’ because they epitomize the barrier to communication that results from the conflation of the process of evolution and our interpretation of life using taxonomy. Opinion may vary regarding the future application of the terms, but we illustrate how the current usage is vague, inconsistent and therefore unhelpful. We conclude that communication across disciplines could be improved by avoiding these terms or acknowledging limitations, and we demonstrate how this can be achieved.

An evolutionary lineage, or line of descent, is the inherent product of evolutionary units replicating in generations over time, and consequently it is a universal feature of all biologically evolving systems

(Cutter, 2013). A ‘species’ is therefore always a taxonomic description of an arbitrarily delineated segment of an evolutionary lineage in time (de Queiroz, 1998, 2007; Sites & Marshall, 2003; Podani, 2013; White, 2013). For different organisms the delineated region will vary in size, scale and duration in time depending upon the nature of the taxonomic paradigm employed, the availability of data (past and present) and the hypothesis under investigation (de Queiroz, 1998, 2007; Sites & Marshall, 2003; White, 2013). However, although a species is artificial, it remains a hypothesis based on empirical observations of an evolutionary lineage (Barraclough & Nee, 2001; de Queiroz, 2011; Strotz & Allen, 2013; Dyneisius & Jansson, 2014; see Fig. 1 for an explanatory metaphor). Philosophically this means that we treat a species as a mental concept based on the material reality of evolutionary lineages (see discussion in Mahner, 1993). Recognizing the consensus of evolutionary lineages is hugely beneficial because

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species. It is arbitrary because the identification of a new species depends upon particular diagnostic thresholds (relative to organisms, scale of observation, data, etc.), which inherently depends upon divergence rather than splitting. Species origination is an epistemological dilemma – is a species classified when a lineage is distinct (but not necessarily separated by gene flow), or when a lineage is separate (but not necessarily distinct)? If a population is morphologically derived with respect to its ancestral population, should it be classified as a separate species based on such difference even if lineage-splitting is not evident? The fact that the answer differs between investigations reflects that the choice is ultimately subjective. So, ‘divergence’ is an increase in difference among evolutionary lineages, ‘splitting’ is the cessation of gene flow between lineages, and ‘speciation’ is the origination of a new species that ideally reflects both divergence and splitting. Divergence and splitting directly describe empirical change among evolutionary lineages, whereas species and speciation are ad hoc classifications applied to interpret the process (see difference between Fig. 1A, B).

The distinction of process and interpretation is advantageous as it recognizes, along with traditional splitting and divergent factors such as isolation and niche separation (Barracough & Nee, 2001; Mallet, 2008b; Maan & Seehausen, 2011), that hybridization of lineages below the species level affects rates of species formation (Abbott *et al.*, 2013; Dynesius & Jansson, 2014). The distinction also reminds us that there is no inherent reason why an increase in the divergence rate, or the molecular evolutionary rate, should incur an increase in the speciation rate (Pennell, Harmon & Uyeda, 2014b). Although there may be a positive correlation between these rates (Webster, Payne & Pagel, 2003; Lanfear *et al.*, 2010; Dowle, Morgan-Richards & Trewick, 2013; Venditti & Pagel, 2014), a split can only be classified as the generation of a new species when a lineage-segment is assigned to the species level. This definition of ‘speciation’ is also preferable as it retains the pure meaning of a new species being generated (de Queiroz, 1998), rather than a technical process that reflexively restricts the meaning of ‘species’. A review of the lineage framework is presented Figure 1 as a metaphor and Table 1 provides a glossary of terms.

### AMBIGUITY OF ANAGENESIS AND CLADOGENESIS

Although the context of evolutionary lineages clarifies the relationship between the evolutionary process and the classification of species, confusion persists due to the ambiguous usage of some terms. In particular, we

observe that the terms of ‘anagenesis’ and ‘cladogenesis’ are frequently used in discussions of evolution and speciation despite the definition and application of the terms varying widely (e.g. Aze *et al.*, 2013; Hunt, 2013; Strotz & Allen, 2013; Patiño *et al.*, 2014; Valente, Etienne & Phillimore, 2014). The terms have generated criticism (e.g. Dubois, 2011), and definition can be vague (e.g. Patiño *et al.*, 2014) or even absent (e.g. Drew & Barber, 2009). This is alarming as the terms are central to many neo- and palaeobiological studies (e.g. Drew & Barber, 2009; Haile-Selassie & Simpson, 2013; Hunt, 2013; Strotz & Allen, 2013; Patiño *et al.*, 2014).

Confusion is in part due to the changing usage of anagenesis and cladogenesis over time (Rensch, 1929, 1959), akin to the conceptual evolution of ‘punctuated equilibrium’ (Eldredge & Gould, 1972; Lieberman & Eldredge, 2014; Pennell, Harmon & Uyeda, 2014a). Anagenesis and cladogenesis were originally coined to differentiate between evolutionary change that leads to the classification of higher taxonomic units such as families (called ‘transspecific evolution’) and ‘narrow-sense’ change at the level of species (‘intraspecific evolution’) (Rensch, 1929, 1959; Glass, 1949). Both terms considered speciation (assuming divergence as a proxy) and were not differentiated by it, nor were they mutually exclusive (Simpson, 1949). Specifically, anagenesis considered a believed trend for increasing complexity in further derived lineages (‘higher evolved organisms’), typically considering morphology (Rensch, 1929, 1959). Cladogenesis was concerned with the evolution of clades – ‘broad’ branches that yielded significant taxonomic diversity (Rensch, 1929, 1959). Cladogenesis was treated as the breadth of an evolutionary tree and anagenesis was the height of branches (where increasing stature was increasing complexity) (Rensch, 1929, 1959). Soon after conception, the terms were applied directly to speciation (Simpson, 1949), and later were integrated with the monophyletic clade and grade concepts of Huxley (1957). Afterwards the terms were merged into the framework of ‘cladistics’ as exemplified by Hennig (Mayr, 1973). Due to the mixing of terminology, ‘cladogenesis’ was inferred to reference the monophyletic branches used as units in cladistics, even though such ‘clades’ have an independent etymology (Cuénot, 1940).

Anagenesis and cladogenesis continue to be used differently by experts among fields. For instance in some biogeography studies, anagenesis is used to refer to founder effects and the formation of endemic species (Patiño *et al.*, 2014; Valente *et al.*, 2014). Similarly, some phylogeographical models refer to speciation caused by geographical mechanisms as cladogenetic events (Shaw *et al.*, 2015). The discussion of punctuated equilibrium in particular has

**Table 1.** A glossary of terms related to anagenesis and cladogenesis

Term	Definition	Type
Evolutionary lineage	A line of descent of evolutionary units (organisms, replicators). All evolutionary units belong to an evolutionary lineage, but our ability to identify particular evolutionary lineages depends upon the availability and scale of data. Evolutionary lineages are continuous through time and can be subdivided down to the level of individual replicators.	Process and pattern
Species	An arbitrary segment of an evolutionary lineage in time classified as a distinct species. Species can be delineated under many different protocols depending upon divergence-based factors such as the data available, studied organism (species criteria) and the hypotheses under investigation.	Classification
Divergence	The accumulation of genetic or phenotypic difference among evolutionary lineages over time that results in distinct variation. Divergence reflects the genetic or phenotypic diversity among lineages, but it does not necessarily require lineage-splitting. Difference can also be measured through time between ancestor and descendant populations.	Process
Lineage-splitting (or lineage-branching)	The cessation of gene flow between populations that causes an evolutionary lineage to divide into two or more. The point at which an interconnected gene pool splits in two. Lineage-splitting can be reversed via hybridization.	Process
Hybridization (or reticulation)	The re-establishment of gene flow between two evolutionary lineages. The inverse process of lineage-splitting. Hybridization can occur between distantly related lineages as well as recently split lineages.	Process
Speciation	Splitting of an evolutionary lineage arbitrarily classified to correspond with the designation of a new species. The origination of a species. The classification of a species often depends upon divergence-based factors such as the data available, studied organism (secondary species criteria) and the hypotheses under investigation.	Classification
Stasis	No significant deviation from an evolutionary state (genetic, phenotypic) over a period of time. Described character states are typically a mean as individuals vary. It reflects divergence that is minor, not sustained, or which does not accumulate. It is driven by stabilizing selection, frequency-dependent selection or selection conflict.	Hypothesis regarding process
Gradualism	A slow, continuous rate of evolutionary change. Some rate variation may occur but it is not overall significant. Originally coined by Hutton (1788), referring to the consistency of change in geology. Expanded by Lyell (1833), in response to Whewell (1831), to describe that the laws of nature (physics, biology) are unchanging, but the rates of geological preservation (e.g. sedimentation, erosion) are highly variable. Co-opted by Darwin (1859) to refer to a continuous rate of change during biological evolution rather than abrupt change.	Hypothesis regarding process

**Table 1.** *Continued*

Term	Definition	Type
Phyletic gradualism	The hypothesis that speciation (and thus divergence and splitting) occurs at a gradualist rate (Eldredge & Gould, 1972). Phyletic gradualism is not interchangeable with gradualism itself as it is the rate applied to speciation.	Hypothesis regarding process and classification
Punctuated equilibrium	Originally coined to refer to geologically abrupt allopatric speciation, alternating with extended periods of morphological and speciation stasis or gradualism in the fossil record (Eldredge & Gould, 1972). It is not mutually exclusive with phyletic gradualism. Nowadays the term has arguably been corrupted and conflated with numerous other hypotheses (Lieberman & Eldredge, 2014; Pennell <i>et al.</i> , 2014a).	Hypothesis regarding process and classification

confused the terms because anagenesis and cladogenesis have been conflated with variation in rates of molecular evolution, speciation and diversification (Benton & Pearson, 2001; Bokma, 2008). Mistakenly, anagenesis is connected or synonymized with phyletic gradualism, gradualism or even stasis (Chaline, 1977; Bokma, 2002; Mattila & Bokma, 2008; Pachut & Anstey, 2012; Lister, 2013; Pearson & Ezard, 2014), and cladogenesis with punctuated change (Bokma, 2002, 2008; Lister, 2013). Rates of speciation and cladogenesis are also incorrectly assumed to be equal (Pennell *et al.*, 2014b). The two terms have even been referred to as ‘modes’ of evolution, suggesting that fundamental mechanisms are described (Pachut & Anstey, 2012; Strotz & Allen, 2013).

In palaeontology, usage is fairly consistent, with ‘cladogenesis’ typically defined as lineage-splitting (branching) (de Queiroz, 1998; Jackson & Cheetham, 1999; Catley, Novick & Shade, 2010; Aze *et al.*, 2013; Bapst, 2013; Futuyma, 2013). Correspondingly, ‘anagenesis’ (or phyletic change) is treated as evolutionary change that occurs within a lineage (Johnson *et al.*, 2012; Pachut & Anstey, 2012; Aze *et al.*, 2013; Bapst, 2013; Futuyma, 2013; Strotz & Allen, 2013), between lineage-splits (e.g. Hunt, 2013; Lister, 2013; Van Bocxlaer & Hunt, 2013). This means that ‘anagenetic change’ is used to mean evolutionary change without lineage-splitting (Jackson & Cheetham, 1999; Catley *et al.*, 2010; Johnson *et al.*, 2012; Bapst, 2013).

Nevertheless, there is a strong tendency to link anagenesis and cladogenesis to speciation. Cladogenesis is commonly considered to be interchangeable with speciation; lineage-splits are assumed to represent the division of one species into two or more (Benton & Pearson, 2001; Mattila & Bokma, 2008; Drew & Barber, 2009; Hunt, 2013; Lister, 2013; Strotz & Allen, 2013; Dynesius & Jansson, 2014; Pearson & Ezard, 2014). In contrast, anagenesis generates conflict as to whether it is a form of speciation (e.g. Jackson &

Cheetham, 1999; Catley *et al.*, 2010; Podani, 2013) or is not (e.g. Bapst, 2013; Ezard *et al.*, 2013; Lister, 2013; Strotz & Allen, 2013; Pennell *et al.*, 2014a). Species can be argued to originate without lineage-splitting because the derived genotype or phenotype of a seemingly un-split lineage is taken to be significantly different from the ancestral state (Benton & Pearson, 2001; Catley *et al.*, 2010; Podani, 2013). Such species are often referred to as ‘chronospecies’ (de Queiroz, 1998; Benton & Pearson, 2001; Haile-Seleassie & Simpson, 2013; White, 2013). These anagenetically produced chronospecies are controversial as they are based on difference of form along a lineage rather than splitting or direct evidence of divergence; they are therefore based on relative character states and particular dates, which can be criticized as an especially arbitrary basis for species delineation (White, 2013, 2014; Vanderlaan & Ebach, 2014).

#### ARE ANAGENESIS AND CLADOGENESIS NECESSARY TERMS?

The varied usages of anagenesis and cladogenesis across biological disciplines is not ideal for clarity, and even the seemingly robust definitions used in palaeontology generate ambiguity between the evolutionary process and species classification. However, the context of evolutionary lineages allows us to disentangle the different concepts conflated under anagenesis and cladogenesis. The insight provided prompts us to question whether anagenesis and cladogenesis are necessary.

#### NOT ALL LINEAGE-SPLITS ARE INFORMATIVE FOR STUDYING LONG-TERM EVOLUTION

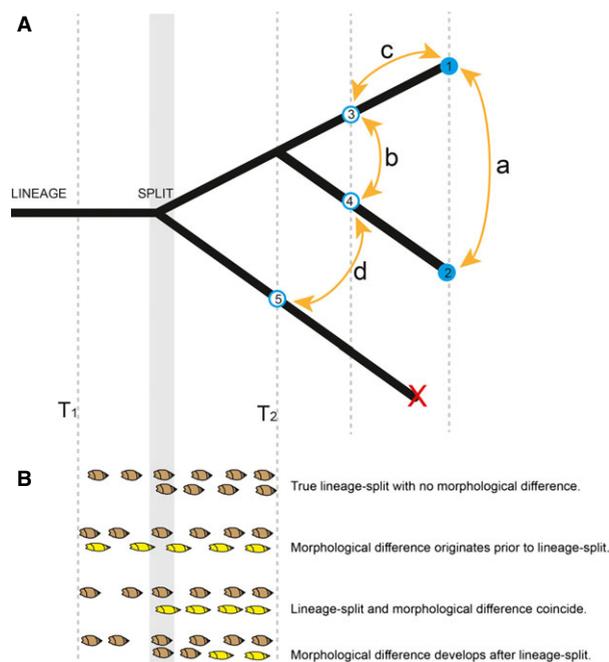
While lineage-splits and evolutionary change between them function as identifiably different concepts, the

descriptive value of this distinction depends upon observation. Problematically, splits are ubiquitous during evolution but not all splits are fixed, and not all splits are of interest. Breaks in gene flow (splits) result in population structuring (Méndez, Tella & Godoy, 2011; Abbott *et al.*, 2013; Heelemann *et al.*, 2014), and can persist for few or many generations (Bhat *et al.*, 2014). Breaks in gene flow are not necessarily absolute nor permanent; two allopatric populations may reconnect (Sternkopf *et al.*, 2010; Abbott *et al.*, 2013), as can so-called incipient species (Bhat *et al.*, 2014), and apparently distinct species can successfully hybridize when opportunity arises (Shiga & Kadono, 2007; Dubois, 2011; Mráz *et al.*, 2012; Pruvost, Hoffman & Reyer, 2013), even millions of years after lineage-splitting (Mallet, 2007; Rothfels *et al.*, 2015). This means that many lineage-splits are masked during evolution and it highlights the importance of hybridization during evolution (Mallet, 2008a; Abbott *et al.*, 2013; Dynesius & Jansson, 2014). Ultimately, gene flow and lineage evolution are also terminated by extinction. Depending upon its frequency, population extinction can generate many splits as it prevents interbreeding among family lines and between metapopulations. This means that lineage-splits are prolific over the course of evolution. However, extinction also erases evidence of lineage-splits because descendants are not available for sampling, which yields long naked branches in molecular phylogenetic reconstructions (Crisp & Cook, 2009; Grandcolas, Nattier & Trewick, 2014). With so many splits occurring and being obscured during evolution it is impossible for all to be identified, and therefore the classification of anagenesis and cladogenesis also becomes untenable. Similarly, partitioning events of divergence with lineage-splits (if they correspond at all) faces the same problem of discrimination.

#### IDENTIFYING LINEAGE-SPLITS REQUIRES GENETIC DATA

The differentiation of anagenesis and cladogenesis via lineage-splitting is popular in palaeontology (e.g. Jackson & Cheetham, 1999; Benton & Pearson, 2001; Crampton & Gale, 2005; Aze *et al.*, 2013; Ezard *et al.*, 2013; Pearson & Ezard, 2014). Using lineage-splits to distinguish anagenesis and cladogenesis creates a quandary for palaeontology, however, because phylogeny can only be inferred from observations of morphology. Analysis of morphological data alone, with no knowledge of gene flow, means that difference must be used to define cladogenesis instead of lineage-splitting. Sequential changes in morphology along a time series, ideally with constrained geography and sufficient sampling (e.g.

Pearson & Ezard, 2014), provide a proxy for an evolutionary lineage (path of genetic inheritance and changing phenotype of a lineage). However, the degree of difference (phenotypic or genetic) is an inadequate proxy for the timing or position of lineage-splitting itself (see Fig. 2A).



**Figure 2.** A, evolutionary lineages and measures of difference. (a) Difference between contemporaneous extant populations (1 and 2) that belong to different lineages. (b) Difference between contemporaneous fossil populations. In this example the samples (3 and 4) belong to the same lineages as in (a) and are therefore part of the same divergence process. (c) Difference between two populations from different times on the same evolutionary lineage. This is an ancestral/derived relationship. In this example Sample 1 is extant and Sample 3 is fossil, but both samples could be fossil populations. Such populations could be treated as chronospecies, as is common in comparisons between fossil samples of different age that are presumed to belong to the same single lineage. (d) Difference between two populations (4 and 5) from different times on different evolutionary lineages. In contrast to (c) these are not ancestral and derived representatives of the same lineage, but in the absence of genetic information it would be impossible to know this. B, identifying lineage-splits without genetic data. Morphological data alone are insufficient to demonstrate lineage-splitting. Morphological difference observed in the fossil record between  $T_1$  and  $T_2$  does not necessarily correspond to a lineage-split (although it does provide a testable hypothesis), and divergence may have occurred before or after any existing split within the intermediate time period.

In palaeontology, difference fails to accurately predict the position of lineage-splits because morphology may diverge before or after a true lineage-split (Fig. 2). Consider, for example, that many species defined by clear genetic cohesion exhibit differing degrees of morphological variation (Blomster, Maggs & Stanhope, 1999; Calsbeek, Smith & Bardeleben, 2007; Hopkins & Tolley, 2011), and that many morphologically cryptic species comprise genetically distinct lineages (e.g. Trewick, 2000; Feldberg *et al.*, 2004; Herbert *et al.*, 2004; Heulskens *et al.*, 2013; see Fig. 2B for an illustration). Simply, without genetic data it is not possible to distinguish within-lineage and between-lineage morphological variation (Van Bocxlaer & Hunt, 2013). Increasing evolutionary time can provide confidence that divergent morphology approximates increasingly well with lineage-splitting, but this is mostly due to lineage-sorting and extinction. Even when divergence is simultaneous with a geological mechanism such as sea-level change, it cannot be used to precisely estimate when a lineage-split may have occurred as such geographical changes can exist for thousands of years (Page & Hughes, 2014). It remains impossible to be certain of when a split occurred and therefore it is difficult to precisely estimate periods of anagenetic and cladogenetic change using morphological data alone (Crampton & Gale, 2005). We agree with Bapst (2013) that it is important to distinguish lineage-splitting, morphological divergence and speciation in palaeontology.

#### SPECIATION IS ARBITRARY

Anagenesis and cladogenesis could be distinguished by classifying lineage-splits to be above or below the species level. This would allow us to ignore the majority of splits that occur during evolution that may not contribute to long-term evolutionary patterns. This would automatically mean that only cladogenesis increases species diversity (Ezard *et al.*, 2012; Strotz & Allen, 2013), whereas anagenesis results in static species diversity (Ezard *et al.*, 2012; Haile-Selassie & Simpson, 2013). Unfortunately this strategy is both circular and arbitrary. The distinction of species level lineages can only be relative as it is dependent upon the studied organism, data available and hypothesis under investigation (Ezard *et al.*, 2013; Haile-Selassie & Simpson, 2013). Even within a single genus, where taxonomic species delineation may have reached a consensus that permits a consistent definition of anagenesis, this approach would not lend itself to comparison across the tree of life. It may be helpful for researchers to use anagenesis and cladogenesis in this relative manner based on the lineage level or evolutionary

persistence, but the limitations must be acknowledged.

Crucially, the distinction is also flawed because it fails to acknowledge that species are arbitrary and that speciation is an artificial concept established on a particular taxonomic paradigm. As species are arbitrarily classified segments of evolutionary lineages they are not discrete states of evolution. At any point a lineage segment can be revised to occur above or below the species level, and correspondingly splits could be reclassified from anagenesis to cladogenesis or vice versa. This type of reciprocal illumination means that the criteria used to define the pattern and process are conflated. Likewise, hybridization can cause lineages to regress below the species level (e.g. Abbott *et al.*, 2013; Bhat *et al.*, 2014; Dynesius & Jansson, 2014), and, because the boundaries of a species do not strictly depend upon lineage-splitting (e.g. species with hybridizing boundaries, ring species, chronospecies), speciation is not a definitive process with a beginning and end. There is no consistency between organisms for distinguishing particular splits as speciation, and there is no agreed point of complete speciation. This already appears to be recognized by authors who have adopted the terms ‘pseudospeciation’ and ‘pseudoextinction’ to describe divergence in the absence of known splitting (e.g. de Queiroz, 1998; Ezard *et al.*, 2012, 2013; Bapst, 2013; Haile-Selassie & Simpson, 2013; Podani, 2013). Species-based definitions of anagenesis and cladogenesis are also post hoc and cannot be applied to currently evolving lineages (i.e. all living lineages) because we cannot predict future splitting, divergence or hybridization.

#### SPECIATION CONSIDERS MORE THAN LINEAGE-SPLITTING

Some lineage-splits are biologically significant because they represent genuine cases of ‘instantaneous speciation’. This can occur, for example, via karyotype changes (Moritz & Bi, 2011), the evolution of parthenogenesis (Abe, 1986), or androgenesis (Scali, Milani & Passamonti, 2012). These scenarios allow neat differentiation of anagenesis and cladogenesis in a species-based manner; however, the majority of species appear to have emerged in a less abrupt manner (Rymer *et al.*, 2010; Claramunt *et al.*, 2012; Near *et al.*, 2012). Most ‘speciation’ is associated with divergence rather than lineage-splitting – new species are usually characterized by unique, identifiable genetic or phenotypic variation compared with related populations (Bapst, 2013). Most often, a particular lineage-split is likely to be merely one step during the change identified as speciation. Focusing on lineage-splitting also distracts from the importance

of lineage hybridization during speciation (Mallet, 2008a, b; Abbott *et al.*, 2013; Sætre, 2013; Dynesius & Jansson, 2014). Even discrete changes related to instantaneous speciation can also be caused by introgression via ploidy changes associated with hybridization (Mallet, 2007; Mráz *et al.*, 2012), and the evolution of reproductive systems such as hybridogenesis (Dubois, 2011; Pruvost *et al.*, 2013).

Even when a lineage-split does represent an abrupt evolutionary change or innovation, many resulting lineages swiftly go extinct. For numerous reasons, systematics generally pays little attention to describing a unique lineage, even if it formed via a single split, unless it persists for a significant length of evolutionary time. The relevance of persistence through time is relative to the studied organism and is dependent upon evolutionary rate estimates that embroil further problems such as gene tree heterogeneity (McCormack *et al.*, 2010; Cutter, 2013), and requires accurate estimations of extinction rates that might be intractable (Barracough & Nee, 2001; Quental & Marshall, 2010; Morlon, Parsons & Plotkin, 2011). For example, a new viral strain may be classified as a species-equivalent within a matter of months, whereas a reproductively isolated group of animals following a karyotype change is unlikely to be classified as a species for thousands or millions of years (Morgan-Richards, Trewick & Wallis, 2001). Species classification is concerned with divergence, hybridization, extinction and informative value as much as splits and monophyly. Overall, it is unhelpful to synonymize cladogenesis (and lineage-splitting) with speciation.

#### UNDERSTANDING EVOLUTION WITHOUT ANAGENESIS AND CLADOGENESIS

To illustrate the frequent redundancy of the terms ‘anagenesis’ and ‘cladogenesis’, we rephrase excerpts from recent studies using fundamental concepts in evolution. In many cases abandoning the terms improves the clarity of reasoning and expression, making research more accessible, and in a few instances it reveals ambiguity or indicates areas for further research. When we replace the terms anagenesis and cladogenesis from recent publications it reveals differences in current usage that are clearly contradictory.

#### *Palaeontology and phylogenetics*

‘A model was fit that allows estimation of anagenetic (within-lineage) evolution, cladogenetic (speciational) change and geographic variation within species.’ (Hunt, 2013).

A model was fit that allows estimation of lineage-splitting above and below the species level, and geographical variation within species.

‘The signal for anagenetic vs. cladogenetic change is subtle: it hinges upon whether the magnitude of divergence between species is more strongly correlated with elapsed time (as predicted by anagenetic change) or with the number of speciation events (as predicted by cladogenetic change) since their common ancestor.’ (Hunt, 2013).

The signal for phylogenetic gradualism vs. punctuated change is subtle: it hinges upon whether the magnitude of divergence between species is more strongly correlated with elapsed time (as predicted by phyletic gradualism) or with the number of speciation events (as predicted by punctuationalism) since their common ancestor.

[They assessed] the relative frequency of anagenesis (evolution within a single evolving lineage) and cladogenesis (lineage branching) in the production of new morphospecies. They conclude that anagenesis is much less prevalent than indicated in our phylogeny.’ (Aze *et al.*, 2013).

[They assessed] the relative frequency of evolutionary change that does and does not generate a net increase in species diversity during the production of new morphospecies. They concluded that evolutionary change that did not lead to a net increase in species diversity was much less prevalent than indicated in our phylogeny.

#### *Biogeography*

‘The theory of “punctuated equilibrium” proposes that species change suddenly during short bursts associated with speciation (“cladogenetic change”). It is best exemplified on oceanic islands, where adaptive radiations have led to spectacular cases of endemic speciation... On islands, the gradual evolution of a new species from a founder event has been called “anagenetic speciation”. This process does not lead to rapid and extensive speciation within lineages, as adaptive radiation may do.’ (Patiño *et al.*, 2014).

The theory of ‘punctuated equilibrium’ proposes that species change suddenly during short bursts associated with speciation. It is best exemplified on oceanic islands [*sic*], where adaptive radiations have led to spectacular cases of endemic speciation... On islands, following a population founder event new species can evolve gradually. This process does not lead to rapid divergence as adaptive radiations may do.

#### CONCLUSION

‘Anagenesis’ and ‘cladogenesis’ are vague and inconsistently defined terms in current research that have been conflated with other hypotheses (Rensch, 1929; Simpson, 1949; Jackson & Cheetham, 1999; Mattila

& Bokma, 2008; Patiño *et al.*, 2014). The most popular, robust definitions are based on the splitting of evolutionary lineages (Jackson & Cheetham, 1999; Catley *et al.*, 2010; Bapst, 2013; Van Bocxlaer & Hunt, 2013), and most authors conflate lineage-splitting with speciation (e.g. Mattila & Bokma, 2008; Drew & Barber, 2009; Hunt, 2013; Dynesius & Jansson, 2014). This is problematic because lineage-splitting is prolific in nature and not all splits are of interest – especially when investigating evolution over long time periods. Splits are common due to population structuring and extinction, and hybridization and extinction mask and reduce the consequence of many splits. Species are arbitrary units, and therefore attempts to differentiate between lineage-splits above and below the species level are relative and dependent upon the studied organism, data available and hypothesis under investigation.

Studying change in species diversity over time is of immense value and is required alongside analysis of the evolutionary process. We emphasize, however, that conflating descriptions of the evolutionary process (lineages, divergence, splitting, hybridization) with taxonomy (species, speciation) does not benefit either line of investigation. Anagenesis and cladogenesis can remain useful terms if future definitions are aware of this separation, even if the terms are accepted to be relative to particular studied organisms. However, if this problem is ignored, anagenesis and cladogenesis will remain a barrier to communication across disciplines, and the terms shall remain replaceable with more fundamental, transparent concepts. Studies of evolution do not need to focus solely on identifying species level change.

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#### REFERENCES

Abbott R, Albach D, Ansell S, Arntzen JW, Baird SJE, Bierne N, Boughman J, Brelsford A, Buerkle CA, Buggs R, Butlin RK, Dieckmann U, Eroukhmanoff F, Grill A, Cahan SH, Hermansen JS, Hewitt G, Hudson AG, Jiggins C, Jones J, Keller B, Marczewski T,

- Mallet J, Martinez-Rodriguez P, Möst M, Mullen S, Nichols R, Nolte AW, Parisod C, Pfennig K, Rice AM, Ritchie MG, Seifert B, Smadja CM, Stelkens R, Szymura JM, Väinölä R, Wolf JBW, Zinner D. 2013. Hybridization and speciation. *Journal of Evolutionary Biology* **26**: 229–246.
- Abe Y. 1986. Taxonomic status of the *Andricus mukaigawae* complex and its speciation with geographic parthenogenesis (Hymenoptera: Cynipidae). *Applied Entomology and Zoology* **21**: 436–447.
- Aze T, Ezard THG, Purvis A, Coxall HK, Stewart DRM, Wade BS, Pearson PN. 2013. Identifying anagenesis and cladogenesis in the fossil record. *Proceedings of the National Academy of Sciences of the United States of America* **110**: E2946.
- Bapst DW. 2013. When can clades be potentially resolved with morphology? *PLoS ONE* **8**: e62312.
- Barracough TG, Nee S. 2001. Phylogenetics and speciation. *Trends in Ecology and Evolution* **16**: 391–399.
- Benton MJ, Pearson PN. 2001. Speciation in the fossil record. *Trends in Ecology and Evolution* **16**: 405–411.
- Bhat S, Amundsen P, Knudsen R, Gjelland KØ, Fevolden S, Bernatchez L, Præbel K. 2014. *PLoS ONE* **9**: e91208.
- Blomster J, Maggs CA, Stanhope MJ. 1999. Extensive intraspecific morphological variation in *Enteromorpha muscoides* (Chlorophyta) revealed by molecular analysis. *Journal of Phycology* **35**: 575–586.
- Bokma F. 2002. Detection of punctuated equilibrium from molecular phylogenies. *Journal of Evolutionary Biology* **15**: 1048–1056.
- Bokma F. 2008. Detection of ‘punctuated equilibrium’ by Bayesian estimation of speciation and extinction rates, ancestral character states, and rates of anagenetic and cladogenetic evolution on a molecular phylogeny. *Evolution* **62**: 2718–2726.
- Calsbeek R, Smith TB, Bardeleben C. 2007. Intraspecific variation in *Anolis sagrei* mirrors the adaptive radiation of Greater Antillean anoles. *Biological Journal of the Linnean Society* **90**: 189–199.
- Catley KM, Novick LR, Shade CK. 2010. Interpreting evolutionary diagrams: when topology and process conflict. *Journal of Research in Science Teaching* **47**: 861–882.
- Chaline J. 1977. Rodents, evolution and prehistory. *Endeavour* **1**: 44–51.
- Claramunt S, Derryberry EP, Brumfield RT, Remsen JV Jr. 2012. Ecological opportunity and diversification in a continental radiation of birds: climbing adaptations and cladogenesis in the Furnariidae. *The American Naturalist* **179**: 649–666.
- Cohan FM. 2002. What are bacterial species? *Annual Review of Microbiology* **56**: 457–487.
- Crampton JS, Gale AS. 2005. A plastic boomerang: speciation and intraspecific evolution in the Cretaceous bivalve *Actinoceramus*. *Paleobiology* **31**: 559–577.
- Crisp MD, Cook LG. 2009. Explosive radiation or cryptic mass extinction? Interpreting signatures in molecular phylogenies. *Evolution* **63**: 2257–2265.

- Cuénot B. 1940.** Remarques sur un essai d'abre généalogique du règne animal. *Comptes Rendus de l'Académie des Sciences* **210**: 23–27.
- Cutter AD. 2013.** Integrating phylogenetics, phylogeography and population genetics through genomes and evolutionary theory. *Molecular Phylogenetics and Evolution* **69**: 1172–1185.
- Darwin CR. 1859.** *On the Origin of Species by means of natural selection, or the preservation of favoured races in the struggle for life*. London: John Murray.
- Dowle EJ, Morgan-Richards M, Trewick SA. 2013.** Molecular evolution and the latitudinal biodiversity gradient. *Heredity* **110**: 501–510.
- Drew J, Barber PH. 2009.** Sequential cladogenesis of the reef fish *Pomacentrus moluccensis* (Pomacentridae) supports the peripheral origin of marine biodiversity in the Indo-Australian archipelago. *Molecular Phylogenetics and Evolution* **53**: 335–339.
- Dubois A. 2011.** Species and 'strange species' in zoology: do we need a 'unified concept of species'? *Comptes Rendus Palevol* **10**: 77–94.
- Dynesius M, Jansson R. 2014.** Persistence of within-species lineages: a neglected control of speciation rates. *Evolution* **68**: 923–934.
- Eldredge N, Gould SJ. 1972.** Punctuated equilibria: an alternative to phyletic gradualism. In: Schopf TJM, ed. *Models in paleobiology*. San Francisco, CA: Freeman, Cooper & Co, 82–115.
- Ezard THG, Pearson PN, Aze T, Purvis A. 2012.** The meaning of birth and death (in macroevolutionary birth-death models). *Biology Letters* **8**: 139–142.
- Ezard THG, Thomas GH, Purvis A. 2013.** Inclusion of a near-complete fossil record reveals speciation-related molecular evolution. *Methods in Ecology and Evolution* **4**: 745–753.
- Feldberg K, Groth H, Wilson R, Schäfer-Verwimp A, Heinrichs J. 2004.** Cryptic speciation in *Herbertus* (Herbertaceae, Jungermannopsida): range and morphology of *Herbertus sendtneri* inferred from nrITS sequences. *Plant Systematics and Evolution* **249**: 247–261.
- Futuyma DJ. 2013.** *Evolution, 3rd edn*. Sunderland, MA: Sinauer Associates.
- Glass B. 1949.** Neuere probleme der abstammungslehre: die transspezifische evolution by Bernhard Rensch. *The Quarterly Review of Biology* **24**: 232–235.
- Grandcolas P, Nattier R, Trewick SA. 2014.** Relict species: a relict concept? *Trends in Ecology and Evolution* **23**: 655–663.
- Haile-Selassie Y, Simpson SW. 2013.** A new species of *Kolpochoerus* (Mammalia: Suidae) from the Pliocene of central Afar, Ethiopia: its taxonomy and phylogenetic relationships. *Journal of Mammalian Evolution* **20**: 115–127.
- Heelemann S, Krug CB, Esler KJ, Poschod P, Reisch C. 2014.** Low impact of fragmentation on genetic variation within and between remnant populations of the typical renosterveld species *Nemesia barbata* in South Africa. *Biochemical Systematics and Ecology* **54**: 59–64.
- Herbert PDN, Penton EH, Burns JM, Janzen DH, Hallwachs W. 2004.** Ten species in one: DNA barcoding reveals cryptic species in the neotropical skipper butterfly *Astraptes fulgerator*. *Proceedings of the National Academy of Sciences of the United States of America* **101**: 14812–14817.
- Heulsken T, Keyse J, Liggins L, Penny S, Treaml EA, Riginos C. 2013.** A novel widespread cryptic species and phylogeographic patterns within several giant clam species (Cardiidae: Tridacna) from the Indo-Pacific Ocean. *PLoS ONE* **8**: e80858.
- Hopkins KP, Tolley KA. 2011.** Morphological variation in the Cape Dwarf chameleon (*Bradypodion pumilum*) as a consequence of spatially explicit habitat structure differences. *Biological Journal of the Linnean Society* **102**: 878–888.
- Hunt G. 2013.** Testing the link between phenotypic evolution and speciation: an integrated palaeontological and phylogenetic analysis. *Methods in Ecology and Evolution* **4**: 714–723.
- Hutton J. 1788.** Theory of the Earth; or, an investigation of the laws observable in the composition, dissolution, and restoration of land upon the globe. *Transactions of the Royal Society of Edinburgh* **1**: 209–304.
- Huxley J. 1957.** The three types of evolutionary process. *Nature* **180**: 454–455.
- Jackson JBC, Cheetham AH. 1999.** Tempo and mode of speciation in the sea. *Trends in Ecology and Evolution* **14**: 72–77.
- Johnson NA, Smith JJ, Pobiner B, Schrein C. 2012.** Why are chimps still chimps? *The American Biology Teacher* **74**: 74–80.
- Lanfear R, Ho SYW, Love D, Bromham L. 2010.** Mutation rate is linked to diversification in birds. *Proceedings of the National Academy of Sciences of the United States of America* **107**: 20423–20428.
- Lieberman BS, Eldredge N. 2014.** What is punctuated equilibrium? What is macroevolution? A response to Pennell et al.. *Trends in Ecology and Evolution* **29**: 185–186.
- Lister AM. 2013.** Speciation and evolutionary trends in quaternary vertebrates. In: Elias S, Mock C, eds. *Encyclopedia of Quaternary Science, 2nd edn*. Amsterdam: Elsevier, 723–732.
- Lyell C. 1833.** *Principles of Geology, being an attempt to explain the former changes of the Earth's surface, by reference to causes now in operation, Vol. 3*. London: John Murray.
- Maan ME, Seehausen O. 2011.** Ecology, sexual selection and speciation. *Ecology Letters* **14**: 591–602.
- Mahner M. 1993.** What is a species? A contribution to the never ending species debate in biology. *Journal of General Philosophy of Science* **24**: 103–126.
- Mallet J. 2007.** Hybrid speciation. *Nature* **446**: 279–283.
- Mallet J. 2008a.** Hybridization, ecological races and the nature of species: empirical evidence for the ease of speciation. *Philosophical Transactions of the Royal Society B: Biological Sciences* **363**: 2971–2986.
- Mallet J. 2008b.** Mayr's view of Darwin: was Darwin wrong about speciation? *Biological Journal of the Linnean Society* **95**: 3–16.
- Mattila TM, Bokma F. 2008.** Extant mammal body masses suggest punctuated equilibrium. *Philosophical Transactions of the Royal Society B: Biological Sciences* **275**: 2195–2199.

- Mayr E. 1973.** Cladistic analysis or cladistic classification? *Journal of Zoological Systematics and Evolutionary Research* **12**: 94–128.
- McCormack JE, Heled J, Delaney KS, Peterson AT, Knowles LL. 2010.** Calibrating divergence times on species trees versus gene trees: implications for speciation history of *Aphelocoma* Jays. *Evolution* **65**: 184–202.
- Méndez M, Tella JL, Godoy JA. 2011.** Restricted gene flow and genetic drift in recently fragmented populations of an endangered steppe bird. *Biological Conservation* **144**: 2615–2622.
- Morgan-Richards M, Trewick SA, Wallis GP. 2001.** Chromosome races with Pliocene origins: evidence from mtDNA. *Heredity* **86**: 303–312.
- Moritz C, Bi K. 2011.** Spontaneous speciation by ploidy elevation: laboratory synthesis of a new clonal vertebrate. *Proceedings of the National Academy of Sciences of the United States of America* **108**: 9733–9734.
- Morlon H, Parsons TL, Plotkin JB. 2011.** Reconciling molecular phylogenies with the fossil record. *Proceedings of the National Academy of Sciences of the United States of America* **108**: 16327–16332.
- Mráz P, Garcia-Jacas N, Gex-Fabry E, Susanna A, Barres L, Müller-Schärer H. 2012.** Allopolyploid origin of highly invasive *Centaurea stoebe* s.l. (Asteraceae). *Molecular Phylogenetics and Evolution* **62**: 612–623.
- Near TJ, Dornburg A, Kuhn KL, Eastman JT, Pennington JN, Patarnello T, Zane L, Fernández DA, Jones CD. 2012.** Ancient climate change, antifreeze, and the evolutionary diversification of Antarctic fishes. *Proceedings of the National Academy of Sciences of the United States of America* **109**: 3434–3439.
- Pachut JF, Anstey RL. 2012.** Rates of anagenetic evolution and selection intensity in Middle and Upper Ordovician species of the bryozoan genus *Peronopora*. *Paleobiology* **38**: 403–423.
- Page TJ, Hughes JM. 2014.** Contrasting insights provided by single and multispecies data in a regional comparative phylogeographic study. *Biological Journal of the Linnean Society* **111**: 554–569.
- Patiño J, Carine M, Fernández-Palacios JM, Otto R, Schaefer H, Vanderpoorten A. 2014.** The anagenetic world of spore-producing land plants. *New Phytologist* **201**: 305–311.
- Pearson PN, Ezard THG. 2014.** Evolution and speciation in the Eocene planktonic foraminifer *Turborotalia*. *Paleobiology* **40**: 130–143.
- Pennell MW, Harmon LJ, Uyeda JC. 2014a.** Is there room for punctuated equilibrium in macroevolution? *Trends in Ecology and Evolution* **29**: 23–32.
- Pennell MW, Harmon LJ, Uyeda JC. 2014b.** Speciation is unlikely to drive divergence rates. *Trends in Ecology and Evolution* **29**: 72–73.
- Podani J. 2013.** Tree thinking, time and topology: comments on the interpretation of tree diagrams in evolutionary/phylogenetic systematics. *Cladistics* **29**: 315–327.
- Pruvost NBM, Hoffman A, Reyer H. 2013.** Gamete production patterns, ploidy, and population genetics reveal evolutionary significant units in hybrid water frogs (*Pelodytes punctatus*). *Ecology and Evolution* **3**: 2933–2943.
- de Queiroz K. 1998.** The general lineage concept of species, species criteria, and the process of speciation. In: Howard DJ, Verlocher SH, eds. *Endless forms: species and speciation*. Oxford: Oxford University Press, 57–75.
- de Queiroz K. 2007.** Species concepts and species delimitation. *Systematic Biology* **56**: 879–886.
- de Queiroz K. 2011.** Branches in the lines of descent: Charles Darwin and the evolution of the species concept. *Biological Journal of the Linnean Society* **103**: 19–35.
- Quental TB, Marshall CR. 2010.** Diversity dynamics: molecular phylogenies need the fossil record. *Trends in Ecology and Evolution* **25**: 434–441.
- Rensch B. 1929.** *Das Prinzip geographischer Rassenkreise und das Problem der Artbildung*. Berlin: Borntraeger.
- Rensch B. 1959.** *Evolution above the species level*. London: Methuen and Co. Ltd.
- Rothfels CJ, Johnson AK, Hovenkamp PH, Swofford DL, Roskam HC, Fraser-Jenkins CR, Windham MD, Pryer KM. 2015.** Natural hybridization between genera that diverged from each other approximately 60 million years ago. *The American Naturalist* **185**: 433–442.
- Rymer PD, Manning JC, Goldblatt P, Powell MP, Savolainen V. 2010.** Evidence of recent and continuous speciation in a biodiversity hotspot: a population genetic approach in southern African gladioli (*Gladiolus*; Iridaceae). *Molecular Ecology* **19**: 4765–4782.
- Sætre GP. 2013.** Hybridization is important in evolution, but is speciation? *Journal of Evolutionary Biology* **26**: 256–258.
- Scali V, Milani L, Passamonti M. 2012.** Revision of the stick insect genus *Leptynia*: description of new taxa speciation mechanism and phylogeography. *Contributions to Zoology* **81**: 25–42.
- Shaw AJ, Shaw B, Johnson MG, Devos N, Stenøien HK, Flatberg KI, Carter BE. 2015.** Phylogenetic structure and biogeography of the Pacific Rim clade of *Sphagnum* subgen. *Subsecunda*: haploid and allopolyploid taxa. *Biological Journal of the Linnean Society* **116**: 295–311.
- Shiga T, Kadono Y. 2007.** Natural hybridization of the two *Nuphar* species in northern Japan: homoploid hybrid speciation in progress. *Aquatic Botany* **86**: 121–131.
- Simpson GG. 1949.** Essay-review of recent works on evolutionary theory by Rensch, Zimmermann, and Schindewolf. *Evolution* **3**: 178–184.
- Sites JW, Marshall JC. 2003.** Delimiting species: a Renaissance issue in systematic biology. *Trends in Ecology and Evolution* **18**: 462–470.
- Sternkopf V, Liebers-Helbig D, Ritz MS, Zhang J, Helbig AJ, de Knijff P. 2010.** Introgressive hybridization and the evolutionary history of the herring gull complex revealed by mitochondrial and nuclear DNA. *BMC Evolutionary Biology* **10**: 348–365.
- Strotz LC, Allen PA. 2013.** Assessing the role of cladogenesis in macroevolution by integrating fossil and molecular evidence. *Proceedings of the National Academy of Sciences of the United States of America* **110**: 2904–2909.

- Trewick SA. 2000.** Mitochondrial DNA sequences support allozyme evidence for cryptic radiation of New Zealand *Peripatoides* (Onychophora). *Molecular Ecology* **9**: 269–281.
- Valente LM, Etienne RS, Phillimore AB. 2014.** The effects of island ontogeny on species diversity and phylogeny. *Philosophical Transactions of the Royal Society B: Biological Sciences* **281**: 20133227.
- Van Bocxlaer B, Hunt G. 2013.** Morphological stasis in an ongoing gastropod radiation from Lake Malawi. *Proceedings of the National Academy of Sciences of the United States of America* **110**: 13892–13897.
- Vanderlaan TA, Ebach MC. 2014.** Systematic biostratigraphy: a solution to problematic classification systems in biostratigraphy. *Palaeoworld* **23**: 105–111.
- Venditti C, Pagel M. 2014.** Plenty of room for punctuational change. *Trends in Ecology and Evolution* **29**: 71–72.
- Webster AJ, Payne RJ, Pagel M. 2003.** Molecular phylogenies link rates of evolution and speciation. *Science* **301**: 478.
- Wei K. 1987.** Multivariate morphometric differentiation of chronospecies in the late Neogene planktonic Foraminifera lineage *Globoconella*. *Marine Micropaleontology* **12**: 183–202.
- Whewell W. 1831.** Review of volume 1 of Lyell's principles of geology. *The British Critic, Quarterly Review, and Ecclesiastical Record* **9**: 180–206.
- White TD. 2013.** Paleoanthropology: five's a crowd in our family tree. *Current Biology* **23**: R112–R115.
- White TD. 2014.** Delimiting species in palaeoanthropology. *Evolutionary Anthropology* **23**: 30–32.