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## COMMENT

# Speciation through the looking-glass

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*Received 2 June 2016; revised 5 July 2016; accepted for publication 6 July 2016*

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We respond to a comment by Allmon WD (2016), who attempted to demonstrate that species are biologically ‘real’ as justification for retaining the terms ‘anagenesis’ and ‘cladogenesis’, which we argue are not necessary for the study of evolutionary biology (Vaux F, Trewick SA & Morgan-Richards M, 2016). Here, we summarize a wealth of literature demonstrating that supposedly separate species introgress frequently, and we clarify that evolutionary lineage-splitting with genotypic and phenotypic divergence (speciation) is not the same as taxonomic classification. The usefulness of the terms anagenesis and cladogenesis requires agreement on their meaning, and this debate reflects a wider dilemma in academic communication: whether to use imprecisely defined jargon or longer sentences with simple words. We favour the latter, because biological evolution operates under straightforward and generalizable principles that should not require complicated descriptions, especially when its study requires collaboration among many disciplines. © 2016 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2016, 00, 000–000.

**KEYWORDS:** anagenetic – cladogenetic – evolutionary lineage – hybrid – introgression – palaeontology – phylogenetics – speciation – species – splitting.

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### INTRODUCTION

In a previous review appearing in the *Biological Journal of the Linnean Society* (Vaux, Trewick & Morgan-Richards, 2016), we considered the usage and meaning of the terms ‘anagenesis’ and ‘cladogenesis’. We observed that the meaning of these terms has changed over time, and that modern usage is highly varied across disciplines and also often ambiguous. We concluded that the terms anagenesis and cladogenesis were not needed to describe evolution or species classification, and that they potentially hamper communication between disciplines. For example, some studies define ‘anagenesis’ as evolutionary change within a species (Johnson *et al.*, 2012; Hunt, 2013; Lister, 2013), whereas others consider the term to be synonymous with gradualism (Ricklefs, 2004; Theriot *et al.*, 2006; Mattila & Bokma, 2008; Pearson & Ezard, 2014). Variation in usage between disciplines is obvious. For example,

many palaeontologists only recognize ‘anagenesis’ when morphospecies do not coexist temporally (Gould, 2001; MacFadden *et al.*, 2012); whereas it is common for biogeographers to consider contemporary but geographically isolated lineages as examples of anagenetic speciation (Rosindell & Phillimore, 2011; Patiño *et al.*, 2014; Valente, Etienne & Phillimore, 2014).

The mode of evolution may be anagenetic if the [first appearance] of the descendant coincides with the [last appearance] of the ancestor within the bounds of the dating precision. (Strotz & Allen, 2013)

A common mode of speciation in ocean islands is by anagenesis, wherein an immigrant arrives and, through time, transforms by mutation, recombination, and drift into a morphologically and genetically distinct species. (López-Sepúlveda *et al.*, 2015)

In a response, Allmon (2016) agrees with much of our review but promotes the treatment of species as being biologically real (Allmon, 2016). This contrasts

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with our approach of treating species classification as arbitrary segments of an evolutionary lineage (Vaux *et al.*, 2016). We welcome the recognition (Allmon, 2016) that ‘change’ and ‘branching’ are suitable substitutes for anagenesis and cladogenesis in many discussions of evolution (Simpson, 1944; Simpson 1953).

## SPECIES AND GENETIC INTROGRESSION

It is not necessary for us to reiterate the thorough exploration of the nature of species and their delimitation (Darwin, 1859; Mayr, 1942; Ghiselin, 1974; Burger, 1975; Mahner, 1993; Mallet, 1995; de Queiroz, 1998; Sites & Marshall, 2003; Hey, 2006; Konstantinidis *et al.*, 2006; Dubois, 2011) because it does not actually address our criticism of ‘anagenesis’ and ‘cladogenesis’, nor does it demonstrate the necessity of the terms. Nonetheless, we do favour the acceptance that species are essentially arbitrary constructs because no concept can be universally and consistently applied to evolving biota (Vaux *et al.*, 2016). In doing so, we follow the simple and well accepted fact identified by Darwin (1859) that species cannot be immutable at the same time as also evolving. Specifically, we observe that, although some species appear to coincide with in vogue concepts, every species is an arbitrary segment of an evolutionary lineage in time (de Queiroz, 1998, 2007; Vaux *et al.*, 2016). We agree with Allmon (2016) that species can be established on the biologically real phenomena of evolutionary lineages [a line of descent of evolutionary units (organisms, replicators)], although the delimitation of a segment (especially in time) remains arbitrary (de Queiroz, 2011). This is because divergence and lineage-splitting are not always concordant and partitions of variation among evolutionary lineages are ultimately of subjective interest to biologists. Practically, one can rarely identify a discrete origin of a species (if such an event ever occurs) and, theoretically, speciation is an infinite process referring to change among related evolutionary lineages.

We agree with a source cited by Allmon (2016) that ‘a generally applicable concept of a species does not yet exist’ (Marie Curie Speciation Network, 2012). The claim that there is a consensus for the definition of a species for ‘at least the biparental animal part of [the living world]’ (Allmon, 2016) is readily falsified (see below) and the need for such a qualifier exposes the inadequacy of the assertion. A unifying concept cannot apply to only a subset of lineages in evolutionary time. Allmon (2016) promotes the view that species are biologically real and, although some taxonomic species are closer representations of

evolutionary lineages than others (Rieseberg, Wood & Baack, 2006), problematic organisms remain abundant (Burger, 1975; Diamond, 1992; Berger & Ogielska, 1994; Domingo *et al.*, 1995; Konstantinidis *et al.*, 2006; Rieseberg *et al.*, 2006; Chan *et al.*, 2012; Fuchs *et al.*, 2015).

Despite previous reviews (Anderson & Stebbins, 1954; Mallet, 2007; Harrison, 2012; Abbott *et al.*, 2013), it appears that the impact of introgression upon speciation and taxonomic classification is not fully appreciated. Introgression originates from two sources: reproduction (or vertical gene transfer) and horizontal gene transfer (Fig. 1). Although hybridization involving reproduction between members of separate lineages sometimes results in nonviable or infertile offspring (Wishart *et al.*, 1988; Allen & Short, 1997; Rieseberg, 1997, Davis *et al.*, 2015), this is not always the case (Burger, 1975; Rieseberg, 1997; Manos, Doyle & Nixon, 1999; Petit *et al.*, 2003; Morgan-Richards *et al.*, 2004; Trewick, Morgan-Richards & Chapman, 2004), even among biparental sexual animals (Derr *et al.*, 1991; Rhymer, Williams & Braun, 1994; Schwarz *et al.*, 2005; Gelberg, 2009; Kraus *et al.*, 2012; The *Heliconius* Genome Consortium, 2012; Cahill *et al.*, 2013; Bull & Sunnucks, 2014; Dowle, Morgan-Richards & Trewick, 2014; Liu *et al.*, 2014; Prüfer *et al.*, 2014; Fuchs *et al.*, 2015; Good *et al.*, 2015; Mckean, Trewick & Morgan-Richards, 2016; Morgan-Richards *et al.*, 2016; Fig 1). Even notoriously infertile first-generation hybrids such as mules (*Equus*) can occasionally be fertile (Allen & Short, 1997), as can lineages that require sexual stimuli or gametes of another lineage (Berger & Ogielska, 1994; Raghianti *et al.*, 2007), and hybridization among distantly related organisms is well documented (Rieseberg & Willis, 2007; Rothfels *et al.*, 2015). Furthermore, hybrid reproduction can be a source of hybrid vigour and it can transfer highly advantageous traits (The *Heliconius* Genome Consortium, 2012).

Horizontal gene transfer (HGT) has had a significant impact over evolutionary time in all major clades of life. Models for the evolution of the eukaryotic cell rely upon HGT and subsequent genetic introgression (Margulis, Dolan & Guerrero, 2000; Georgiades & Raoult, 2011, 2012), and abundant evidence demonstrates that organellar DNA is continuously transferred to the nucleus (Blanchard & Lynch, 2000; Stegemann *et al.*, 2003), as well as between organelles (Goremykin *et al.*, 2009). Other prokaryotic endosymbionts (organisms within the cells of another) are also absorbed (Gonella *et al.*, 2015) and undergo HGT (Kondo *et al.*, 2002; Husnik *et al.*, 2013; Sloan *et al.*, 2014; Wybouw *et al.*, 2014), and viruses facilitate HGT between themselves and eukaryotic host genomes (Bejarano *et al.*, 1996;

Löwer, Löwer & Kurth, 1996; Mallet *et al.*, 2004; Carrat & Flahault, 2007; Herniou *et al.*, 2013; Gasmi *et al.*, 2015). Even the most reproductively discrete, biparental, sexual animals are therefore continuously introgressing with DNA of prokaryotic and viral origin. HGT is near-constant in bacteria via direct cell-to-cell exchange, indirect environmental exchange between cells, and indirect exchange between cells via viral infection (Ochman, Lawrence & Groisman, 2000; Krebes *et al.*, 2014). In many mutualistic and parasitic situations, nonvectored HGT involves all combinations of animals, bacteria, fungi, and plants, including both nuclear and organellar DNA (Vaughn *et al.*, 1995; Groth, Hansen & Piškur, 1999; Davis & Wurdack, 2004; Woloszynska *et al.*, 2004; Hall, Brachat & Dietrich, 2005; Moran & Jarvik, 2010; Yoshida *et al.*, 2010; Acuña *et al.*, 2012; Kim *et al.*, 2014; Nikolaidis, Doran & Cosgrove, 2014; Wybouw *et al.*, 2014). HGT is observed between animal hosts and transmissible cancers (Metzger *et al.*, 2016; Strakova *et al.*, 2016) and syncytial growth (nuclei sharing among cells) in fungi also provides the potential for HGT and viable interspecies genetic mosaics (*in sensu* Roper *et al.*, 2013). These genetic exchanges often produce functional genes (Mallet *et al.*, 2004; Nikolaidis *et al.*, 2014), and associated traits often have the potential to be significantly advantageous and are of clear taxonomic interest (Bock, 2010; Moran & Jarvik, 2010; Herniou *et al.*, 2013; Nikolaidis *et al.*, 2014; Crisp *et al.*, 2015; Gasmi *et al.*, 2015). Resulting changes in the evolutionary trajectory of a lineage affect the overall pattern of lineage-splitting and divergence among populations, meaning that introgression does not merely result in gene tree heterogeneity. A plethora of examples illustrate how reproduction and HGT maintain introgression and unclear boundaries for species classification (Fig. 1); species do not ‘maintain their separateness’ (Allmon, 2016).

In some ways, we and Allmon are speaking past one another because perceptions of the status of species are sensitive to the resolution at which they are observed. At the scale typically used to investigate trends in biodiversity, species can appear coherent and separate. Most taxonomic work depends on arbitrary distinctions made by experts with the primary objective of defining distinct units. However, at a closer range where lineage-splitting and divergence are studied in detail, it often becomes apparent that such coherence is superficial. Under most definitions (Aze *et al.*, 2013; Lister, 2013; Strotz & Allen, 2013), it is this scale of lineage-splitting at which periods of anagenesis and cladogenesis are defined, and thus where problems arise. Similar scale differences also affect the study of topics such as evolutionary stasis, where

a trait can appear morphologically static over long periods of time but less so over a shorter time period with more frequent sampling intervals (Hunt, 2012).

‘When I use a word’, Humpty Dumpty said in a rather scornful tone, ‘it means just what I choose it to mean – neither more nor less’.

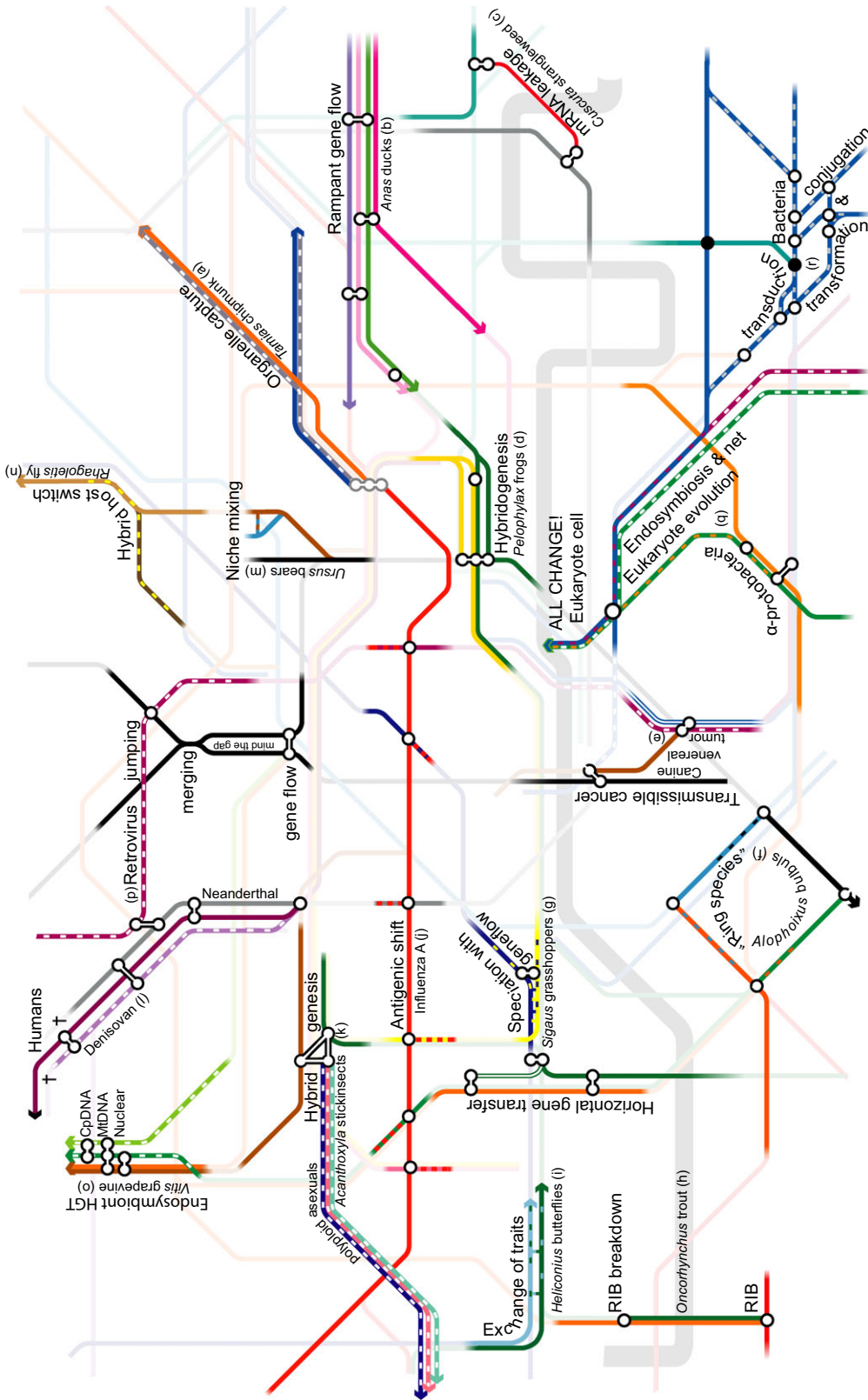
(Lewis Carroll, 1871 in *Through The Looking Glass*)

[also aptly quoted in Harrison, 2012]

Allmon (2016) conflates species classification (and delimitation) with speciation by suggesting that we are not interested in studying speciation. Although seemingly an arid enterprise, clarification of terms used in evolutionary biology is needed for the intelligent exploration of biology. We explicitly stated that the classification (and observation) of a species depends upon divergence-based factors and the hypothesis of interest (Vaux *et al.*, 2016). What this means is that the origination of species as a classified taxon is arbitrary, although the process of lineage-splitting and divergence that creates the diversity used to describe it is biologically real (and interesting). When most evolutionary biologists refer to ‘speciation’, we assume that they mean the latter process, and not the pedantic and arbitrary delimitation of a taxon. The process is of interest because it considers the biological evidence available (genetic variation, phenotypic variation, selection), whereas taxonomy is deciding when and how to assign names based, usually on a subset of that evidence. The fact that we treat a species as an arbitrary concept does not prevent hypothesis testing, the study of lineage-splitting, divergence or diversification rates, or investigation of the fossil record (Darwin, 1859).

## ANAGENESIS AND CLADOGENESIS

There are many instances where palaeontological evidence provides estimates of when lineage-splits must have occurred (e.g. Strotz & Allen, 2013; Pearson & Ezard, 2014; Kimura, Flynn & Jacobs, 2016) and we also agree that palaeontologically recognized species can be comparable to living taxa (even if this is difficult to demonstrate) on a lineage divided into segments in time (de Queiroz, 1998; Kimura *et al.*, 2016). However, morphological crypsis leading to underestimation of diversity is not the only problem for the morphological identification of extinct species. The treatment of ‘estimates of species and speciation rates [as] *minimum* estimates’ (Allmon, 2016) is flawed because there are also cases of taxonomic over-splitting in palaeontology that leads to overestimation of diversity (Hills *et al.*, 2012; Aze *et al.*, 2013).



**Figure 1.** Hybrid reproduction (vertical gene transfer) and horizontal gene transfer (HGT) result in frequent introgression among evolutionary lineages, which reveals that putative taxonomic species do not remain separate and that their delimitation is ultimately subjective. Here, we illustrate some of the range of processes that have so far been identified, citing examples in the primary and review literature (letter codes a - r refer to references listed in Supporting Information Table S1, and many other examples are provided therein). Re-purposing an unrelated network demonstrates that modes of introgression are so prolific and diverse that almost any example can be illustrated by an arbitrary selection of intersecting lines. Note that the network relationships demonstrate gene flow but not phylogeny or a scaled representation of change through time.

Despite lengthy discussion of species classification in the fossil record, Allmon (2016) does not define the terms or address the actual concern of our review: the ability to consistently define (and delineate in time) anagenesis (phyletic change) and cladogenesis (divergence concurrent with lineage-splitting) based on morphological evidence alone. Morphological divergence and lineage-splitting are not necessarily concordant. Even in palaeontological studies incorporating genetic data, estimates that utilize independent loci within a lineage will provide a range of dates (rather than a single estimate) for a lineage-split. This is problematic for the delimitation of anagenesis and cladogenesis because most palaeontological definitions assume their mutual exclusivity (Aze *et al.*, 2013; Lister, 2013).

Never use a long word when a diminutive one will do.  
(William Safire, 1979 in *On Language*, *New York Times Magazine*)

The claim that we have only demonstrated ‘disparate usage by a few modern authors’ (Allmon, 2016) is inaccurate because our review cited many recent papers that vary in the meaning given to anagenesis and cladogenesis (Mattila & Bokma, 2008; Drew & Barber, 2009; Catley, Novick & Shade, 2010; Dubois, 2011; Johnson *et al.*, 2012; Pachut & Anstey, 2012; Aze *et al.*, 2013; Bapst, 2013; Futuyma, 2013; Hunt, 2013; Podani, 2013; Strotz & Allen, 2013; Dynesius & Jansson, 2014; Pearson & Ezard, 2014; Patiño *et al.*, 2014; Valente *et al.*, 2014). For this contemporary variation to exist, the terms cannot have remained consistent ‘for more than half a century’, as Allmon (2016) suggests. We do not think this variation should be ignored because previous studies also discuss the problematic meaning of the terms (Benton & Pearson, 2001; Dubois, 2011) and also because textbooks and educational research demonstrate that definitions vary (Catley *et al.*, 2010; Johnson *et al.*, 2012; Futuyma, 2013), indicating that this ambiguity may be inherited by future scientists. If we follow the definition used by Simpson (1944), as suggested by Allmon (2016), why do we need multiple words for ‘branching’ and ‘phyletic change’? What is the necessity of redundant terminology (likewise with ‘tokogenesis’ for gene flow; Allmon, 2016)?

## CONCLUSIONS

Ultimately, the necessity of terms such as anagenesis and cladogenesis reflects a wider problem in academic communication. Researchers will decide

whether to use complex terminology (giving each term the meaning they choose) or longer sentences with simple words. Biological evolution fundamentally operates under the basic principles of variation, selection, and heritability, which can be effectively modelled using even simple descriptions such as the univariate breeder’s equation ( $R = Sh^2$ ). Although this process generates rich complexity in nature, we consider that descriptions of biological evolution need not require complex and alienating language. We do not expect everyone to agree with our views on anagenesis and cladogenesis, although we hope it can at least be agreed that the terms in their current state are problematic for the communication of science and, in future, authors should clearly express their definition of the terms or otherwise avoid them.

## ACKNOWLEDGEMENTS

We are grateful for the constructive criticism and feedback from the reviewers Warren D. Allmon and William Miller III. We thank the *Biological Journal of the Linnean Society* and the editor John A. Allen for the opportunity to publish our response. This work was supported by the Royal Society of New Zealand Te Apārangi Marsden Fund grant (12-MAU-008).

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## SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article:

**Table S1.** Primary and review references for evidence of particular modes of genetic introgression via reproduction [vertical gene transfer (VGT)] and horizontal gene transfer (HGT), most of which are illustrated by single examples in Fig. 1. Only a small amount of the available literature is listed, and we deliberately focus upon examples from biparental sexual animals.