
COMMENT

Speciation through the looking-glass

FELIX VAUX*, STEVEN A. TREWICK and MARY MORGAN-RICHARDS

Ecology Group, Institute of Agriculture and Environment, Massey University, Palmerston North, New Zealand

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

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*, 2017, **120**, 480–488.

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

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

*Corresponding author. E-mail: f.vaux@massey.ac.nz

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; Ragghianti *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, Brachet & 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).

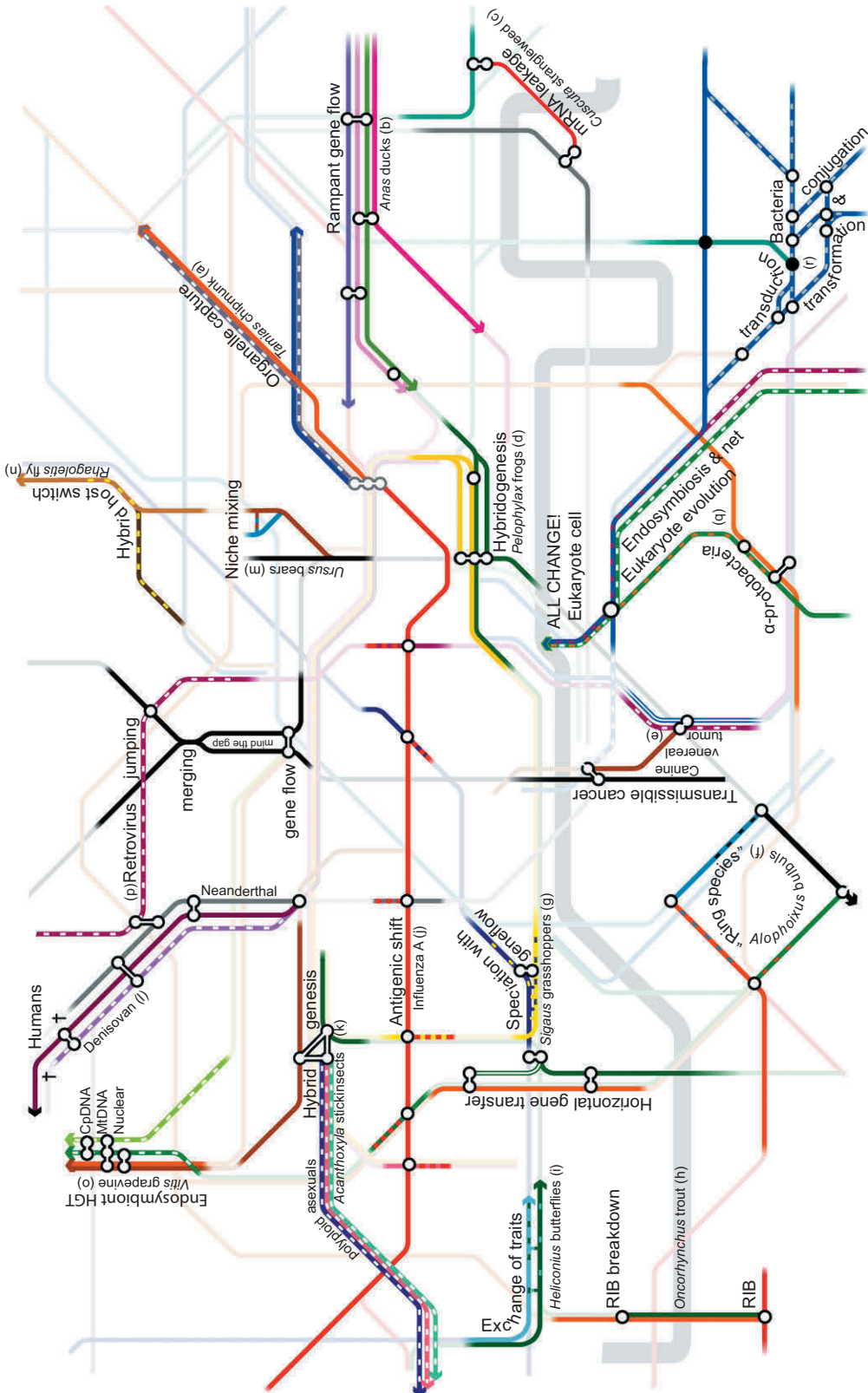


Figure 1. Hybrid reproduction (vertical gene transfer) and horizontal gene transfer (HGT) result in frequent introgression among evolutionary lineages, which reveals that putative taxonomic species do not remain separate and that their delimitation is ultimately subjective. Here, we illustrate some of 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 Aparangi Marsden Fund grant (12-MAU-008).

REFERENCES

- Abbott R, Albach D, Ansell S, Arntzen JW, Baird SJE, Bierre 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.
- Acaña R, Padilla BE, Flórez-Ramos C, Rubio JD, Herrera JC, Benavides P, Lee S, Yeats TH, Egan AN, Doyle JJ, Rose JKC. 2012. Adaptive horizontal transfer of a bacterial gene to an invasive insect pest of coffee. *Proceedings of the National Academy of Sciences of the United States of America* **109**: 4197–4202.
- Allen WR, Short RV. 1997. Interspecific and extraspecific pregnancies in Equids: anything goes. *Journal of Heredity* **88**: 384–392.
- Allmon WD. 2016. Species, lineages, splitting, and divergence: why we still need ‘anagenesis’ and ‘cladogenesis’. *Biological Journal of the Linnean Society* doi:10.1111/bij.12885

- Anderson E, Stebbins GL Jr. 1954.** Hybridization as an evolutionary stimulus. *Evolution* **8**: 378–388.
- 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.
- Bejarano ER, Khashoggi A, Witty M, Lichtenstein C. 1996.** Integration of multiple repeats of geminiviral DNA into the nuclear genome of tobacco during evolution. *Proceedings of the National Academy of Sciences of the United States of America* **93**: 756–764.
- Benton MJ, Pearson PN. 2001.** Speciation in the fossil record. *Trends in Ecology and Evolution* **16**: 405–411.
- Berger L, Ogielska M. 1994.** Spontaneous haploid–triploid mosaicism in the progeny of a *Rana* kl. *esculenta* female and *Rana lessonae* males. *Amphibia-Reptilia* **15**: 143–152.
- Blanchard JL, Lynch M. 2000.** Organellar genes: why do they end up in the nucleus? *Trends in Genetics* **16**: 315–320.
- Bock R. 2010.** The give-and-take of DNA: horizontal gene transfer in plants. *Trends in Plant Science* **15**: 11–22.
- Bull JK, Sunnucks P. 2014.** Strong genetic structuring without assortative mating or reduced hybrid survival in an onychophoran in the Tallaganda State Forest region, Australia. *Biological Journal of the Linnean Society* **111**: 589–602.
- Burger WC. 1975.** The species concept in *Quercus*. *Taxon* **24**: 45–50.
- Cahill JA, Green RE, Fulton TL, Stiller M, Jay F, Ovsyanikov N, Salamzade R, St. John J, Stirling I, Slatkin M, Shapiro B. 2013.** Genomic evidence for island population conversion resolves conflicting theories of polar bear evolution. *PLOS Genetics* **9**: e1003345.
- Carrat F, Flahault A. 2007.** Influenza vaccine: the challenge of antigenic shift. *Vaccine* **25**: 6852–6862.
- Catley KM, Novick LR, Shade CK. 2010.** Interpreting evolutionary diagrams: when topology and process conflict. *Journal of Research in Science Teaching* **47**: 861–882.
- Chan JZ-M, Halachev MR, Loman NJ, Constantinidou C, Pallen MJ. 2012.** Defining bacterial species in the genomic era: insights from the genus *Acinetobacter*. *BMC Microbiology* **12**: 302.
- Crisp A, Boschetti C, Perry M, Tunnacliffe A, Micklem G. 2015.** Expression of multiple horizontally acquired genes is a hallmark of both vertebrate and invertebrate genomes. *Genome Biology* **16**: 50.
- Darwin CR. 1859.** *On the origin of species*. London: John Murray.
- Davis CC, Wurdack KJ. 2004.** Host-to-parasite gene transfer in flowering plants: phylogenetic evidence from Malpighiales. *Science* **305**: 676–678.
- Davis BW, Seabury CM, Brashear WA, Li G, Roelke-Parker M, Murphy WJ. 2015.** Mechanisms underlying mammalian hybrid sterility in two feline interspecies models. *Molecular Biology and Evolution* **32**: 2534–2546.
- Derr JN, Hale DW, Ellsworth DL, Bickham JW. 1991.** Fertility in an F₁ hybrid of white-tailed deer (*Odocoileus virginianus*) × mule deer (*O. hemionus*). *Journal of Reproduction and Fertility* **93**: 111–117.
- Diamond JM. 1992.** Horrible plant species. *Nature* **360**: 627–628.
- Domingo E, Holland JJ, Biebricher C, Eigen M. 1995.** Quasi-species: the concept and the word. In: Gibbs AJ, Calisher CH, García-Arenal F, eds. *Molecular basis of virus evolution*. Cambridge: Cambridge University Press, 181–191.
- Dowle EJ, Morgan-Richards M, Treweek SA. 2014.** Morphological differentiation despite gene flow in an endangered grasshopper. *BMC Evolutionary Biology* **14**: 216.
- 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.
- Fuchs J, Ericson PGP, Bonillo C, Couloux A, Pasquet E. 2015.** The complex phylogeography of the Indo-Malayan *Alophoixus* bulbuls with the description of a putative new ring species complex. *Molecular Ecology* **24**: 5460–5474.
- Futuyma DJ. 2013.** *Evolution, 3rd edn*. Sunderland, MA: Sinauer Associates.
- Gasmi L, Boulain H, Gauthier J, Hua-Van A, Musset K, Jakubowska AK, Aury J-M, Volkoff A-N, Huguet E, Herrero S, Drezen J-M. 2015.** Recurrent domestication by Lepidoptera of genes from their parasites mediated by Bracoviruses. *PLOS Genetics* **11**: e1005470.
- Gelberg HB. 2009.** Purkinje fiber dysplasia (histiocytoid cardiomyopathy) with ventricular noncompaction in a savannah kitten. *Veterinary Pathology* **46**: 693–697.
- Georgiades K, Raoult D. 2011.** The rhizome of *Reclinomonas americana*, *Homo sapiens*, *Pediculus humanus* and *Saccharomyces cerevisiae* mitochondria. *Biology Direct* **6**: 55.
- Georgiades K, Raoult D. 2012.** How microbiology helps define the rhizome of life. *Frontiers in Cellular and Infection Microbiology* **2**: 60.
- Ghiselin MT. 1974.** A radical solution to the species problem. *Systematic Zoology* **23**: 536–544.
- Gonella E, Pajoro M, Marzorati M, Crotti E, Mandrioli M, Pontini M, Bulgari D, Negri I, Sacchi L, Chouaia B, Daffonchio D, Alma A. 2015.** Plant-mediated interspecific horizontal transmission of an intracellular symbiont in insects. *Scientific Reports* **5**: 15811.
- Good JM, Vanderpool D, Keeble S, Bi K. 2015.** Negligible nuclear introgression despite complete mitochondrial capture between two species of chipmunks. *Evolution* **69**: 1961–1972.
- Goremykin VV, Salamini F, Valesco R, Viola R. 2009.** Mitochondrial DNA of *Vitis vinifera* and the issue of

- rampant horizontal gene transfer. *Molecular Biology and Evolution* **26**: 99–110.
- Gould SJ. 2001.** The interrelationship of speciation and punctuated equilibrium. In: Cheetham AH, Jackson JBC, Lidgard S, McKinney FK, eds. *Evolutionary patterns: growth, form, and tempo in the fossil record*. Chicago, IL: University of Chicago Press, 207–208.
- Groth C, Hansen J, Piskur J. 1999.** A natural chimeric yeast containing genetic material from three species. *International Journal of Systematic Bacteriology* **49**: 1933–1938.
- Hall C, Brachat S, Dietrich FS. 2005.** Contribution of horizontal gene transfer to the evolution of *Saccharomyces cerevisiae*. *Eukaryotic Cell* **4**: 1102–1115.
- Harrison RG. 2012.** The language of speciation. *Evolution* **66**: 3643–3657.
- Herniou EA, Huguet E, Thézé J, Bézier A, Periquet G, Drezen J-M. 2013.** When parasitic wasps hijacked viruses: genomic and functional evolution of polydnviruses. *Philosophical Transactions of the Royal Society Series B, Biological Sciences* **368**: 20130051.
- Hey J. 2006.** On the failure of modern species concepts. *Trends in Ecology and Evolution* **21**: 447–450.
- Hills SFK, Crampton JS, Treweek SA, Morgan-Richards M. 2012.** DNA and morphology unite two species and 10 million year old fossils. *PLoS ONE* **12**: e52083.
- Hunt G. 2012.** Measuring rates of phenotypic evolution and inseparability of tempo and mode. *Paleobiology* **38**: 351–373.
- 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.
- Husnik F, Nikoh N, Koga R, Ross L, Duncan RP, Fujie M, Tanaka M, Satoh N, Bachtrog D, Wilson ACC, von Dohlen CD, Fukatsu T, McCutcheon JP. 2013.** Horizontal gene transfer from diverse bacteria to an insect genome enables a tripartite nested mealybug symbiosis. *Cell* **153**: 1567–1578.
- Johnson NA, Smith JJ, Pobiner B, Schrein C. 2012.** Why are chimps still chimps? *The American Biology Teacher* **74**: 74–80.
- Kim G, LeBlanc ML, Wafula EK, dePamphilis CW, Westwood JH. 2014.** Genomic-scale exchange of mRNA between a parasitic plant and its hosts. *Science* **345**: 808–811.
- Kimura Y, Flynn LJ, Jacobs LL. 2016.** A palaeontological case study for species delimitation in diverging fossil lineages. *Historical Biology* **28**: 189–198.
- Kondo N, Nikoh N, Ijichi N, Shimada M, Fukatsu T. 2002.** Genome fragment of *Wolbachia* endosymbiont transferred to X chromosome of host insect. *Proceedings of the National Academy of Sciences of the United States of America* **99**: 14281–14285.
- Konstantinidis KT, Ramette A, Tiedje JM. 2006.** The bacterial species definition in the genomic era. *Philosophical Transactions of the Royal Society Series B, Biological Sciences* **361**: 1929–1940.
- Kraus RHS, Kerstens HHD, van Hooft P, Mergens H, Elmberg J, Tsvey A, Sartakov D, Soloviev SA, Crooijmans RPMA, Groenen MAM, Ydenberg RC, Prins HHT. 2012.** Widespread horizontal genomic exchange does not erode species barriers among sympatric ducks. *BMC Evolutionary Biology* **12**: 45.
- Krebs J, Didelot X, Kennemann L, Suerbaum S. 2014.** Bidirectional genomic exchange between *Helicobacter pylori* strains from a family in Coventry, United Kingdom. *International Journal of Medical Microbiology* **304**: 1135–1146.
- 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.
- Liu S, Lorenzen ED, Fumagalli M, Li B, Harris K, Xiong Z, Zhou L, Sand Koreneliussen T, Somel M, Babbitt C, Wray G, Li J, He W, Wang Z, Fu W, Xiang X, Morgan CC, Doherty A, O'Connell MJ, Zhang G, Nielsen R, Willerslev E, Wang J. 2014.** Population genomics reveal recent speciation and rapid evolutionary adaptation in polar bears. *Cell* **157**: 785–794.
- López-Sepúlveda P, Takayama K, Greimler J, Crawford DJ, Peñailillo P, Baeza M, Ruiz E, Kohl G, Tremetsberger K, Gatica A, Letelier L, Novoa P, Novak J, Stuessy TF. 2015.** Progressive migration and anagenesis in *Drimys confertifolia* of the Juan Fernández Archipelago, Chile. *Journal of Plant Research* **128**: 73–90.
- Löwer R, Löwer J, Kurth R. 1996.** The viruses in all of us: characteristics and biological significance of human endogenous retrovirus sequences. *Proceedings of the National Academy of Sciences of the United States of America* **93**: 5177–5184.
- MacFadden BJ, Oviedo LH, Seymour GM, Ellis S. 2012.** Fossil horses, orthogenesis, and communicating evolution in museums. *Evolution: Education and Outreach* **5**: 29–37.
- 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. 1995.** A species definition for the modern synthesis. *Trends in Ecology and Evolution* **10**: 294–299.
- Mallet J. 2007.** Hybrid speciation. *Nature* **446**: 279–283.
- Mallet F, Bouton O, Prudhomme S, Cheynet V, Oriol G, Bonnaud B, Lucotte G, Duret L, Mandrand B. 2004.** The endogenous retroviral locus ERVWE1 is a bona fide gene involved in hominoid placental physiology. *Proceedings of the National Academy of Sciences of the United States of America* **101**: 1731–1736.
- Manos PS, Doyle JJ, Nixon KC. 1999.** Phylogeny, biogeography, and processes of molecular differentiation in *Quercus* subgenus *Quercus* (Fagaceae). *Molecular Phylogenetics and Evolution* **12**: 333–349.
- Margulis L, Dolan MF, Guerrero R. 2000.** The chimeric eukaryote: origin of the nucleus from the karyomastigont in amitochondriate protists. *Proceedings of the National Academy of Sciences of the United States of America* **97**: 6954–6959.
- Mattila TM, Bokma F. 2008.** Extant mammal body masses suggest punctuated equilibrium. *Philosophical Transactions of the Royal Society Series B, Biological Sciences* **275**: 2195–2199.
- Mayr E. 1942.** *Systematics and the origin of species from the viewpoint of a zoologist*. New York, NY: Columbia University Press.
- McKean NE, Treweek SA, Morgan-Richards M. 2016.** Little or no gene flow despite F₁ hybrids at two

- interspecific contact zones. *Ecology and Evolution* **6**: 2390–2404.
- Moran NA, Jarvik T. 2010.** Lateral transfer of genes from fungi underlies carotenoid production in aphids. *Science* **328**: 624–627.
- Metzger MJ, Villalba A, Carballal MJ, Iglesias D, Sherry J, Reinisch C, Muttray AF, Baldwin SA, Goff SP. 2016.** Widespread transmission of independent cancer lineages within multiple bivalve species. *Nature* **534**: 705.
- Morgan-Richards M, Trewick SA, Chapman HM, Krahulcova A. 2004.** Interspecific hybridization among *Hieracium* species in New Zealand: evidence from flow cytometry. *Heredity* **93**: 34–42.
- Morgan-Richards M, Hills SKF, Biggs PJ, Trewick SA. 2016.** Sticky genomes: using NGS to test hybrid speciation hypothesis. *PLoS ONE* **11**: e0154911.
- Network MCS. 2012.** What do we need to know about speciation? *Trends in Ecology and Evolution* **27**: 27–39.
- Nikolaidis N, Doran N, Cosgrove DJ. 2014.** Plant expansins in bacteria and fungi: evolution by horizontal gene transfer and independent domain fusion. *Molecular Biology and Evolution* **31**: 376–386.
- Ochman H, Lawrence JG, Groisman EA. 2000.** Lateral gene transfer and the nature of bacterial innovation. *Nature* **405**: 299–304.
- 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.
- 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.
- Petit RJ, Bodénès C, Ducouso A, Roussel G, Kremer A. 2003.** Hybridization as a mechanism of invasion in oaks. *New Phytologist* **161**: 151–164.
- Podani J. 2013.** Tree thinking, time and topology: comments on the interpretation of tree diagrams in evolutionary/phylogenetic systematics. *Cladistics* **29**: 315–327.
- Prüfer K, Racimo F, Patterson N, Jay F, Sankararaman S, Sawyer S, Heinze A, Renaud G, Sudmant PH, de Filippo C, Li H, Mallick S, Dannemann M, Fu Q, Kircher M, Kuhlwilm M, Lachmann M, Meyer M, Ongyerth M, Siebauer M, Theunert C, Moorjani P, Pickrell J, Mullikin JC, Vohr SH, Green RE, Hellmann I, Johnson PLF, Blanche H, Cann H, Kitzman JO, Shendure J, Eichler EE, Lein ES, Bakken TE, Golovanova LV, Doronichev VB, Shunkov MV, Derevianko AP, Viola B, Slatkin M, Reich D, Kelso J, Pääbo S. 2014.** The complete genome sequence of a Neanderthal from the Altai Mountains. *Nature* **505**: 43–49.
- 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.
- Ragghianti M, Bucci S, Marracii S, Casola C, Mancino G, Hotz H, Geux G-D, Plötner J, Uzzell T. 2007.** Gametogenesis of intergroup hybrids of hemiclinal frogs. *Genetical Research* **89**: 39–45.
- Rhymer JM, Williams MJ, Braun MJ. 1994.** Mitochondrial analysis of gene flow between New Zealand mallards (*Anas platyrhynchos*) and grey ducks (*A. superciliosa*). *The Auk* **111**: 970–978.
- Ricklefs RE. 2004.** Cladogenesis and morphological diversification in passerine birds. *Nature* **430**: 338–341.
- Rieseberg LH. 1997.** Hybrid origins of plant species. *Annual Review of Ecology and Systematics* **28**: 359–389.
- Rieseberg LH, Willis JH. 2007.** Plant speciation. *Science* **317**: 910–914.
- Rieseberg LH, Wood TE, Baack EJ. 2006.** The nature of plant species. *Nature* **440**: 524–527.
- Roper M, Simonin A, Hickey PC, Leeder A, Glass NL. 2013.** Nuclear dynamics in a fungal chimera. *Proceedings of the National Academy of Sciences of the United States of America* **110**: 12875–12880.
- Rosindell J, Phillimore AB. 2011.** A unified model of island biogeography sheds light on the zone of radiation. *Ecology Letters* **14**: 552–560.
- 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. *American Naturalist* **185**: 433–442.
- Schwarz D, Matta BM, Shakir-Botteri NL, McPherson BA. 2005.** Host shift to an invasive plant triggers rapid animal hybrid speciation. *Nature* **436**: 546–549.
- Simpson GG. 1953.** *Major features of evolution*. New York, NY: Columbia University Press.
- Simpson GG. 1944.** *Tempo and mode in evolution*. New York, NY: Columbia University Press.
- Sites JW, Marshall JC. 2003.** Delimiting species: a Renaissance issue in systematic biology. *Trends in Ecology and Evolution* **18**: 462–470.
- Sloan DB, Nakabachi A, Richards S, Qu J, Canchi Murali S, Gibbs RA, Moran NA. 2014.** Parallel histories of horizontal gene transfer facilitated extreme reduction of endosymbiont genomes in sap-feeding insects. *Molecular Biology and Evolution* **31**: 857–871.
- Stegemann S, Hartmann S, Ruf S, Bock R. 2003.** High-frequency gene transfer from the chloroplast genome to the nucleus. *Proceedings of the National Academy of Sciences of the United States of America* **100**: 8828–8833.
- Strakova A, Leathlobhair MN, Wang G-D, Yin T-T, Airikkala-Otter I, Allen JL, Allum KM, Banske-Issa L, Bisson JL, Domracheva AC, de Castro KF, Corrigan AM, Cran HR, Crawford JT, Cutter SM, Keenan LD, Donelan EM, Faramade IA, Reynoso EF, Fotopoulou E, Fruean SN, Gallardo-Arrieta F, Glebova O, Häfelin**

- Manrique R, Henriques JJGP, Ignatenko N, Koenig D, Lanza-Perea M, Lobetti R, Lopez Quintana AM, Losfelt T, Marino G, Martincorena I, Martínez Castañeda S, Martínez-López MF, Meyer M, Nakanwagi B, De Nardi AB, Neunzig W, Nixon SJ, Onsare MM, Ortega-Pacheco PM, Pye RJ, Reece JF, Rojas Gutierrez J, Sadia H, Schmeling SK, Shamanova O, Ssuna RK, Steenland-Smit AE, Svitich A, Thoya Ngoka I, Viřálaru BA, de Vos AP, de Vos JP, Walkinton O, Wedge DC, Wehrle-Martinez AS, van der Wel MG, Widdowson SAE, Murchison EP. 2016. Mitochondrial genetic diversity, selection and recombination in a canine transmissible cancer. *Elife* **5**: e14552.
- 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.
- The Heliconius Genome Consortium. 2012. Butterfly genome reveals promiscuous exchange of mimicry adaptations among species. *Nature* **487**: 94–98.
- Theriot EC, Fritz SC, Whitlock C, Conley DJ. 2006. Late Quaternary rapid morphological evolution of an endemic diatom in Yellowstone Lake, Wyoming. *Paleobiology* **32**: 38–54.
- Trewick SA, Morgan-Richards M, Chapman HM. 2004. Chloroplast DNA diversity of *Hieracium pilosella* (Asteraceae) introduced to New Zealand: reticulation, hybridization, and invasion. *American Journal of Botany* **91**: 73–85.
- 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.
- Vaughn JC, Mason MT, Sper-Whitis G, Kuhlman P, Palmer JD. 1995. Fungal origin by horizontal transfer of a plant mitochondrial group I intron in the chimeric Cox1 gene of *Peperomia*. *Journal of Molecular Evolution* **41**: 563–572.
- Vaux F, Trewick SA, Morgan-Richards M. 2016. Lineages, splits and divergence challenge whether the terms anagenesis and cladogenesis are necessary. *Biological Journal of the Linnean Society* **117**: 165–176.
- Wishart WD, Hrudka F, Schmutz SM, Flood PF. 1988. Observations on spermatogenesis, sperm phenotype, and fertility in white-tailed x mule deer hybrids and a yak x cow hybrid. *Canadian Journal of Zoology* **66**: 1664–1671.
- Wolozynska M, Bocer T, Mackiewicz P, Janska H. 2004. A fragment of chloroplast DNA was transferred horizontally, probably from non-eudicots, to mitochondrial genome of *Phaseolus*. *Plant Molecular Biology* **56**: 811–820.
- Wybouw N, Dermauw W, Tirry L, Stevens C, Grbić M, Feyereisen R, Van Leeuwen T. 2014. A gene horizontally transferred from bacteria protects arthropods from host plant cyanide poisoning. *Elife* **3**: e02365.
- Yoshida S, Maruyama S, Nozaki H, Shirasu K. 2010. Horizontal gene transfer by the parasitic plant *Striga hermonthica*. *Science* **328**: 1128.

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.