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1 **More grist for the mill?: Species delimitation in the genomic era and its**  
2 **implications for conservation**

3  
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19  
20 **Abstract**

21  
22 Species delimitation is one of the most contested areas in modern biology, with  
23 widespread disagreement about almost every aspect of the definition and  
24 implementation of the “species” label. While this debate is intellectually  
25 stimulating, it also has real implications for conservation, where its impacts on  
26 taxonomic inflation or inertia can mean that specific populations receive adequate  
27 conservation measures or are ignored. Recently, the rise of next generation  
28 sequencing and phylogenomics has revolutionised phylogenetic understanding of  
29 many organismal groups but has simultaneously highlighted the porosity of  
30 genomes in terms of admixture across previously delineated species barriers. The  
31 extraordinary power of genomic data is increasingly being used to delineate  
32 species, and several publications in this domain have recently attracted significant  
33 attention and criticism. Here we revisit the question of species delimitation, but  
34 from a genomic context. We ask how and whether the large amounts of data  
35 provided by genomic methods can resolve the longstanding discussion on the  
36 validity and application of phylogenetic and allied species concepts, and how some  
37 recent examples can inform this debate. We argue that conserving adaptive  
38 potential is a priority for conservation, and no single species concept currently  
39 does that adequately on its own. Genomic data holds the potential to add  
40 unprecedented detail, but frequently falls short of this potential.

41  
42  
43  
44 ***INFLATION OR INERTIA?***

45  
46 Due to the pivotal role of the species as the most important unit of biodiversity,  
47 conservation planning must be based on a good understanding of species number,  
48 diversity and endemism, measurements that only make sense within the context  
49 of consistent taxonomic classifications (Isaac, Mallet and Mace, 2004; Zachos *et al.*,  
50 2013). However, as a result of the many different epistemological views on the

51 species concept (e.g. Avise and Ball, 1990; Wheeler and Platnick, 2000; Baker and  
52 Bradley, 2006), and due to the gradual process of evolutionary divergence, there  
53 is a continuum of genomic divergence patterns and estimates for which different  
54 researchers would consider speciation to be ‘complete’ (DeQueiroz, 1998). Some  
55 evolutionary biologists have classified populations as the same species unless  
56 strong evidence to the contrary exists, *e.g.* reproductive incompatibility or  
57 reciprocal monophyly (with the archaic term ‘lumpers’; Heller *et al.*, 2013). The  
58 genealogical concordance method of phylogenetic species recognition (often  
59 known as the genealogical species concept, or GSC; Avise and Ball, 1990; Baum  
60 and Shaw, 1995), as well as the Biological species concept (BSC), often result in a  
61 high threshold of species recognition. The GSC usually considers two populations  
62 to be designated species only when they are “*isolated long enough [that] all gene-*  
63 *genealogies will be concordant*” (emphasis ours; Baum and Shaw, 1995). This  
64 concept has been criticized for its stringent nature, as it, for example conflicts with  
65 the observed incomplete lineage sorting and admixture between the genomes of  
66 some well-recognised species (for example lineage sorting in Ursine bears,  
67 Kutschera *et al.*, 2014; and apes, Mailund *et al.*, 2014; and introgression between  
68 chimpanzees and bonobos deManuel *et al.*, 2016; within gulls; Sonsthagen *et al.*  
69 2016; and geese, Ottenburghs *et al.* 2017).

70  
71 In contrast, other evolutionary biologists set the threshold for recognition of new  
72 species, much lower (*i.e.* so-called ‘splitters’, the past antonym of ‘lumpers’) whose  
73 approach is usually via the use of the Phylogenetic Species Concept (PSC). The PSC  
74 defines species as “*the smallest aggregation of (sexual) populations or (asexual)*  
75 *lineages diagnosable by a unique combination of character states*” (Wheeler and  
76 Platnick, 2000). This method of classification is much less stringent and it could  
77 be argued that any intra-specific population genetic structure should result in the  
78 fulfilment of the requirement of “*a unique combination of character states*”. It has  
79 therefore been criticized for increasing the number of recognized species beyond  
80 what would seem justified, known as ‘taxonomic inflation’ (Heller *et al.*, 2013;  
81 Zachos 2013; Zachos *et al.* 2013).

82  
83 Recently, Gippoliti *et al.*, (2017) describe the opposing argument that ‘taxonomic  
84 inertia’ is actually more detrimental to conservation, highlighting the case of  
85 African ungulates. They argue that the history of African ungulate taxonomic  
86 classification has been dominated by ‘lumpers’ who, when faced with difficult  
87 taxonomic decisions, have avoided the situation by assigning a large number of  
88 subspecies or genetic lineage labels. According to the authors, this has led to a  
89 disproportionately small number of ungulate species being recognised in Africa  
90 (despite Africa being by far the leading continent in terms of recognized ungulate  
91 species richness (Heywood 2010)). Key to the argument of Gippoliti *et al.* (2017)  
92 is a survey by Morrison *et al.*, (2009), which showed that taxonomic splitting has  
93 a positive effect on conservation. Morrison *et al.*, (2009) identify numerous  
94 situations where a change in taxonomy has led to increased conservation efforts.  
95 One representative example is the California gnatcatcher, *Poliioptila californica*.  
96 Morrison *et al.*, (2009) highlight the increase in conservation funding (better  
97 habitat protection and monitoring programs) that this species received after  
98 recognition of its species status. However, a change in protection (conservation)  
99 in this study was defined in Morrison *et al.*, (2009) as “*increased or decreased*

100 *monitoring of any kind*”, as well as “*increased or decreased funding for research on*  
101 *the respective organism*”. This argument only considers the organism in question,  
102 not conservation actions as a whole. This overlooks an obvious concern, namely  
103 that conservation resources are finite (although not necessarily constant), and  
104 that resources allocated to one species do not necessarily benefit others. This is  
105 the ‘Agony of choice’ argument (Isaac, Mallet and Mace, 2004), which refers to the  
106 greater challenge of assigning limited conservation resources between higher  
107 numbers of taxa. Gippoliti *et al.*, (2017) also state that there is “no evidence for  
108 negative effects of taxonomic splitting on conservation”. It could be argued,  
109 however, that this hypothesis would be very difficult to empirically support either  
110 way. It is not currently known precisely how much is being spent on conservation  
111 globally (McCarthy *et al.*, 2012), let alone the relative amounts that are being spent  
112 on each taxonomic group. **In an ideal scenario, all units of diversity would be**  
113 **conserved however, even in countries that allocate a relatively large budget to**  
114 **conservation efforts, this is rarely possible (Malaney and Cook, 2013), and even a**  
115 **prioritization approach may not be being practised (especially when it conflicts**  
116 **with other political priorities [Migration, Denver Post]). It therefore seems very**  
117 **likely** that conserving the eleven species of klipspringer proposed by Groves and  
118 Grubb (2011) as separate taxa would require more resources than conserving the  
119 one klipspringer species, *Oreotragus oreotragus*, commonly recognised (e.g.  
120 Kingdon, 2013). In conservation (specifically in the IUCN context), a particular  
121 machinery comes into play when a new species becomes known, including making  
122 species status assessments, a species survival plan including *in situ* and *ex situ*  
123 measures (if deemed necessary for the species). All of these obviously require  
124 resources, and this is before even expending resources on the actual, practical  
125 conservation measures for the species.

126  
127 Another argument for why over-splitting may be detrimental for particular  
128 taxonomic groups, Frankham *et al.*, (2012) focused on three widely used species  
129 concepts: the Biological (Mayr 1942, 1963), the Evolutionary (ESC; Simpson,  
130 1951, 1961; Wiley, 1978) and Phylogenetic (Eldredge and Cracraft, 1980; Cracraft,  
131 1997) Species Concepts. Frankham *et al.*, (2012) emphasised the point that  
132 diagnosably different population units are not intrinsically reproductively  
133 isolated (**the importance of reproductive isolation is discussed in detail later**), and  
134 that this is particularly relevant for small, allopatric populations. This is because  
135 the time in which a population attains alleles that make it distinguishable in e.g.  
136 multivariate genetic space will be proportional to their effective population sizes  
137 ( $N_e$ ), and may be very short if  $N_e$  is low. The implication of this is that populations  
138 of the greatest conservation concern may be more likely to be diagnosed by the  
139 PSC. **It should be noted that this argument is only referring to the conservation**  
140 **implications of the species concept used, and not an assessment of which is**  
141 **“correct”**.

142  
143 It seems clear that both “taxonomic inflation” and “taxonomic inertia” could be  
144 detrimental to conservation. This is because implicit in those descriptors is an  
145 assumption that the populations in question have been artificially “grouped” more  
146 or less than what would be ideal under any given criterion (also keeping in mind  
147 that different criteria might not lead to the same “ideal” grouping!). Conservation  
148 (and in particular its genetic component) is predominantly a pragmatic discipline,

149 which for populations threatened with extinction, a primary concern is assessing  
150 whether re-joining populations (and therefore gene flow) is possible and deciding  
151 whether those populations *should* still be connected. These decisions are usually  
152 based on taxonomy, with the assumption that it is related to whether the  
153 populations are likely to be reproductively isolated, and to what extent they have  
154 unique adaptations to their local environment. **However, this assumption may be**  
155 **correct or incorrect, depending on the premise of the species criterion used (see**  
156 **“WHICH SPECIES CONCEPT BEST CONSERVES ADAPTIVE POTENTIAL?”). This**  
157 **raises three important distinctions that need to be made when a decision is**  
158 **reached about what constitutes a species:**

- 159 1. Distinguishing species
- 160 2. How they are diagnosed
- 161 3. Classification, i.e. how they are ranked

162 Point one is an ontological question, i.e. what one considers a species to actually  
163 *be*. Point two is a question of implementation: a technical/financial hurdle that is  
164 imposed based on the species concept that is chosen. Point three could be referred  
165 to as a “convention of organization”, and depends on where any given organization  
166 chooses to delimit taxonomic boundaries. This framework links to the difference  
167 between a concept and a criterion, two terms that are frequently conflated in  
168 species discussions: A species concept relates to point one, and a species criterion  
169 relates to point two (De Queiroz 1998).

170  
171 Some authors may argue that certain criteria are invalid because they do not  
172 identify units that they believe to be “real” species, however this can be countered  
173 by defining criteria as a concept, and thereby essentially redefining what a species  
174 *is* to fit in with a given criterion. It has been argued that all species concepts have  
175 a single common concept, namely that species can be equated with “segments of  
176 population-level lineages” (De Queiroz 1998; De Queiroz 1999), or groups of  
177 organisms with their own “independent evolutionary fate and historical  
178 tendencies” (Mayden, 1997). Under this framework, the so-called General Lineage  
179 Concept (GLC), it is argued that alternative species concepts are either variations  
180 of the GLC, or criteria of it. While this is a compelling argument, in the sense that  
181 it relates to ontology, it could still be considered a matter of opinion.

182  
183 In an attempt to make the definition of species less arbitrary, increasingly  
184 sophisticated methods have been produced to delineate species. Developments in  
185 coalescent theory has allowed for the investigation of lineage diversification  
186 (Yang, 2015). Other methods for molecular species identification include Bayes  
187 factor-based species delimitation (Grummer et al. 2014). These methods, based  
188 on different criteria/theories, test species boundaries in a comparative way  
189 (Toussaint et al. 2016). However, the multispecies coalescent has also been  
190 criticised for only being a method to “delimit structure, not species” (Sukumaran  
191 and Knowles 2017).

192  
193 Further discussion on which of the various species concepts is “correct” remains  
194 outside the scope of this manuscript. Rather we seek to ask if, and how, genomic  
195 data have influenced the operational nature of the various species concepts.  
196 Specifically, has the increasing resolving power of genomic tools i) been used to  
197 invoke the chosen species concept (we focus on the PSC and BSC) more readily,

198 or, ii) led to a more conservative approach to species delineation due to the  
 199 complex interaction of admixture, incomplete lineage sorting, and demographic  
 200 history that is increasingly being detected. We also revisit the question of the link  
 201 between species concepts and adaptive potential, and whether new genomic data  
 202 has had an influence on this question. We focus on case studies from the recent  
 203 literature (Table 1), which highlight how species delineations have been applied  
 204 to date. These studies either use what could broadly be described as the BSC or  
 205 the PSC (here synonymous with “lumping” and “splitting”, respectively) in order  
 206 to justify their species delineations.

207  
 208

**Table 1.** Summary of the genomic evidence used in our case studies

Study	Reference	Genomic resources	Analyses	Species criteria used
<b>Newly proposed species</b>				
<b>Giraffe</b>	Fennessey et al (2016)	One draft genome	<ul style="list-style-type: none"> <li>Phylogeny</li> <li>Genetic structure (Using 7 intron loci and mitochondrial DNA)</li> </ul>	Unique genetic character states (PSC)
<b>Orang-utan</b>	Nater et al. (2017)	37 resequenced genomes	<ul style="list-style-type: none"> <li>Phylogeny</li> <li>Genetic structure</li> <li>Demographic history</li> <li>Morphology</li> </ul> (Genetic data from two, and morphological data from one <i>Pongo tapanulienis</i> individual[s])	Unique genetic and morphological character states (PSC)
<b>Finless porpoise</b>	Zhou et al (2018)	48 resequenced genomes	<ul style="list-style-type: none"> <li>Phylogeny</li> <li>Genetic structure</li> <li>Demographic history</li> <li>Signatures of selection</li> </ul>	Reproductive isolation (BSC)
<b>Darwin’s finch spp.</b>	Lamichhane et al (2017)	47 resequenced genomes, genomic data from 180 individuals from previous study	<ul style="list-style-type: none"> <li>Phylogeny</li> <li>Morphology</li> <li>Pedigree assessments</li> <li>Demographic history</li> <li>Phenotype-genotype associations</li> </ul>	Reproductive isolation (BSC)
<b>Currently recognised species</b>				
<b>Stickleback spp.</b>	Ravinet et al (2018)	27 resequenced genomes	<ul style="list-style-type: none"> <li>Phylogeny</li> <li>Demographic history</li> <li>Detection of introgression</li> <li>Genetic structure</li> <li>Signatures of selection</li> </ul>	Species claim not made in this study, but well-recognised as different species with reproductive isolation, and ecological and phenotypic differences (BSC)

209  
 210  
 211

**NEWLY PROPOSED SPECIES**

212 *Giraffe*

213 Recently, Fennessey *et al.*, (2016), produced a draft genome for the giraffe (*Giraffa*  
 214 *camelopardalis*), and analysed nuclear and mitochondrial sequences from 105  
 215 individuals from all currently recognized subspecies. In identifying four distinct  
 216 genetic clusters they concluded that “*population genetic, phylogenetic, and*  
 217 *network analyses of nuclear sequences demonstrate that the giraffe is genetically*  
 218 *well structured into four distinct species*”. However, this conclusion was based on  
 219 only two mitochondrial and seven intron loci. It contrasts with a previous genetic  
 220 study of giraffe, which used 14 microsatellite loci from 381 individuals to identify

221 six distinct clusters (Brown *et al.*, 2007), without designating these clusters to  
222 species. Therefore, both studies were based on a relatively small number of loci  
223 that showed varying genetic structure but reached different conclusions. This  
224 could be explained by variation among loci with different realisations of stochastic  
225 lineage sorting, an effect that while still possible for large numbers of loci, is more  
226 likely to be observed in studies using relatively few (Orozco-terWengel *et al.*,  
227 2011). The operational approach used in Fennessey *et al.*, (2016) could be  
228 described as conforming to the PSC, as the genetic structure was used to justify a  
229 “*unique combination of character states*” (i.e. nuclear alleles), present in each of  
230 the populations (or species).

231

232 Of all the examples presented below, the findings presented in Fennessey *et al.*,  
233 (2016) have probably received the most attention to date, reviving the debate on  
234 giraffe taxonomy and conservation. Bercovitch *et al.*, (2017) listed seven points of  
235 concern about the original authors’ interpretation of their results. Their concerns  
236 included a criticism of the lack of concordance between mitochondrial and nuclear  
237 phylogenies, few loci, and a disagreement that assignment to separate genetic  
238 clusters was a sufficient indicator of species designation. They concluded that the  
239 study of Fennessey *et al.*, (2016) should only be regarded as one perspective on  
240 giraffe taxonomy. On the lack of power of the nuclear dataset used, Fennessey *et al.*,  
241 (2017) argued that “*Compared to microsatellite data, DNA sequences allow*  
242 *estimating divergence times*”. Fennessey *et al.*, (2016), however, did not estimate  
243 population divergence times, only sequence divergence times, which, incidentally,  
244 can also be estimated with microsatellites (e.g. Hey, 2010). The response by  
245 Bercovitch *et al.*, (2017) also highlighted different criteria for species delimitation  
246 than Fennessey *et al.*, (2016, 2017). Whilst Fennessey *et al.* (2016, 2017) advocate  
247 diagnosability using (neutral) genetic markers as the primary criteria for species  
248 delineations, Bercovitch *et al.* (2017) placed a greater emphasis on phenotypic  
249 and behavioural characteristics. They stated that: “*Coat color patterns are linked*  
250 *to specific gene complexes with mutations leading to variation subject to natural*  
251 *selection... Phenotypic traits regulate mating patterns and sexual selection that*  
252 *establish a foundation for the recognition species concept*”.

253

254 Ultimately, Fennessey *et al.*, (2016) used limited genetic data to detect genetic  
255 structure and sequence divergence criteria, which were then equated with species  
256 divergence by applying the PSC. However, the process of lineage sorting under  
257 plausible demographic and selection models was not considered, nor their  
258 influence in the context of the limited number of markers used. **A follow-up study  
259 using a larger set of nuclear markers has since been carried out, which confirms  
260 that gene-flow between the four proposed species is very low (Winter et al. 2018).  
261 However, it appears that in this situation the argument is predominantly of an  
262 ontological nature, and so may not have run its course yet.**

263

264 *Orang-utan*

265 Nater *et al.*, (2017) recently described the genomic diversity of a population of  
266 orangutans from the species’ southernmost range limit in Sumatra (Batang Toru).  
267 They concluded that the Batang Toru population was sufficiently distinct to  
268 warrant being named a new species. This conclusion was based on morphometric,  
269 behavioural and genomic evidence from 33-37 individuals (the morphological

270 analysis could only use a single Batang Toru specimen). Using Approximate  
271 Bayesian Computation modelling of demography, it was estimated that the  
272 northern Sumatra population split from the older Batang Toru ~3.4 million years  
273 ago (mya), but maintained gene flow until 10-20 thousand year ago (kya). The  
274 authors also point out that there are many instances of ongoing gene flow between  
275 taxa that are recognised as distinct, well-established species. In light of this, Nater  
276 *et al.*, (2017) use the species definition that describes species as “a population (or  
277 group of populations) with fixed heritable differences from other such populations  
278 (or groups of populations)”, effectively invoking the PSC.

279  
280 The morphological evidence which led to the conclusion of a new orang-utan  
281 species was based on a single specimen from the population in question (and  
282 genomic evidence based on two). Any criticisms of the validity/robustness of this  
283 conclusion could be centred around the question of whether a single specimen can  
284 be considered representative of the whole population. Nater *et al.*, (2017) point  
285 out that numerous species have been identified based on a single type specimen  
286 in the past. Based on genomics, the authors were able to show that these two  
287 orangutan populations had fixed heritable differences with an estimated  
288 termination of gene-flow from/to the proposed new species 10 – 20 kya. Yet, Nater  
289 *et al.* (2017) did not assess if these SNPs were associated with adaptive differences  
290 between the populations. Thus, although Nater *et al.* (2017) used genomics to  
291 enhance their power to apply the PSC with greater resolution, they did not use it  
292 to attempt to understand the speciation process in any mechanistic sense. The  
293 conclusions reached by Nater *et al.*, (2017) has not been accepted by all in the  
294 scientific community, particularly by proponents of the BSC (e.g  
295 [https://whyevolutionistrue.wordpress.com/2017/11/03/a-new-species-of-](https://whyevolutionistrue.wordpress.com/2017/11/03/a-new-species-of-orangutan-i-doubt-it/)  
296 [orangutan-i-doubt-it/](https://whyevolutionistrue.wordpress.com/2017/11/03/a-new-species-of-orangutan-i-doubt-it/)). Nater *et al.*, (2017) pointed out that determining if these  
297 populations are reproductively isolated or not is not possible, due to their  
298 allopatric distribution. **One potential solution that was not used by Nater *et al.***  
299 **(2017) is the Tobias criteria (Tobias *et al.* 2010). This uses sympatric species pairs**  
300 **to set thresholds for delineating allopatric taxa.** It seems likely that despite the  
301 large number of features investigated, and analytical methods applied, this  
302 approach will still fall short of the expectations of many proponents of the BSC.

303  
304 In short, the orang-utan paper represents a case in which a large panel of the  
305 genomic tools available have been applied to address the question of population  
306 divergence. While presumably adding detailed information about the historical  
307 processes, it does not attempt to analyse adaptive differences, nor to answer  
308 whether maintaining these two populations of orang-utan as separate would  
309 maximize the adaptive potential going forward.

310

### 311 *Finless porpoise*

312 Zhou *et al.*, (2018) investigated speciation in finless porpoises, which have  
313 traditionally been classified as a single species, *Neophocaena phocaenoides*.  
314 Finless porpoises exist as three geographic populations or subspecies, two marine  
315 (Indo-Pacific) and one freshwater population (Yangtze River). Zhou *et al.*, (2018)  
316 identified several candidate genes related to hypoxia that show strong evidence  
317 of directional selection. They also estimated divergence of the Yangtze River  
318 population at 5,000 – 40,000 years ago. These findings led them to conclude that



319 “significant population differentiation, lack of gene flow, and unique adaptive  
320 divergence in the Yangtze finless porpoise make it clear that the Yangtze finless  
321 porpoise is genetically and reproductively isolated from its marine counterpart and  
322 thus represents an incipient species”.

323

324 The main aspect that differentiates the porpoise case study from that of the  
325 orangutan is the term “unique adaptive divergence”. By identifying selection  
326 signatures in several candidate genes that are the result of diversifying selection  
327 to two different ecosystems, Zhou *et al.*, (2018) found plausible mechanistic  
328 evidence for an instance of incipient speciation. Whilst the orang-utan study by  
329 Nater *et al.*, (2017) showed phenotypic differences between the two proposed  
330 species, no evidence was presented to demonstrate that this divergence was  
331 adaptive, and therefore driving speciation. This highlights the issue that, although  
332 genomic methods for identifying selection in natural populations has advanced  
333 considerably over recent years, it is still challenging to do this with limited  
334 numbers of samples.

335

336 *Darwin’s finches*

337 Lamichhaney *et al.*, (2017) documented a remarkable example of hybrid  
338 speciation from its origin to reproductive isolation in a hybrid between two  
339 Darwin’s finch species (*Geospiza fortis* and *G. conirostris*). This hybrid lineage was  
340 shown to breed endogamously from the second generation onwards, with  
341 transgressive segregation of bill morphology, a trait that is known to be under  
342 strong selective pressure in these species. This study demonstrates that  
343 reproductive isolation can occur rapidly, in as little as three generations. This  
344 species classification was therefore based on reproductive isolation of the new  
345 hybrid finch lineage from its parent lineages, aka the BSC.

346

347 *Prima facie*, the question of a new species of Darwin’s finch seems very simple:  
348 These species exist in sympatry, and were observed to stop interbreeding, a  
349 situation clearly fulfilling the criteria of distinct species under the BSC. However,  
350 Hill and Zink (2018) firstly notes that three to four generations may not be enough  
351 time to determine if the new lineage is ephemeral or not, and secondly that  
352 phenotypic differences observed may be highly plastic. The conclusions of  
353 Lamichhaney *et al.*, (2017) are strengthened by the fact that they also investigated  
354 the genetic basis for bill dimension, a morphological trait that is implicated in  
355 driving ecological success and reproductive isolation of the big bird lineage. By  
356 observing correlations between the ALX1 and HMGA2 loci with morphometrics,  
357 they were able to use genomics to provide evidence for genetic adaptation to a  
358 new environment. It seems unlikely that the level of observational evidence that  
359 they used will be practical for most wild species, a common criticism of the  
360 practicality of the BSC (Amato and Russello, 2014). However, there are genomic  
361 approaches that can bypass these challenges for many taxa. For example, relatives,  
362 pedigrees, and local ancestry tracts can be identified so that reproductive isolation  
363 over the last few generations can be inferred from genetic data (e.g. as carried out  
364 in humans, Ko and Nielsen, 2017). This could serve as an alternative to  
365 observational studies.

366

367 This is not to say that there are not conceptual criticisms that can be made of the  
368 BSC regardless of how it is operationalized (e.g. related to instances of viable  
369 hybrids between organisms well-recognised to be different species (Nater *et al.*,  
370 2017)). As discussed earlier, a full discussion of this is beyond the scope of this  
371 manuscript, however, genomic tools are at least allowing us to be able to better  
372 quantify and understand the relevance of these instances (even when we only  
373 have low coverage data or few individuals, Schaefer *et al.*, 2017).

374

375 Genomic and other data increasingly show that these hybridization and  
376 introgression events can no longer be classed as a rare or insignificant: they are  
377 now being recognised as both common and important evolutionary mechanisms,  
378 including sometimes being implicated in the adaptive advantages to a newly  
379 colonised environment (e.g. invertebrates, Pogson, 2016; plants, Ru *et al.*, 2016;  
380 and vertebrates, Barbato *et al.*, 2017).

381

### 382 **THE ROLE OF HYBRIDISATION IN SPECIES DESIGNATION**

383

384 Hybridization is ubiquitous in nature. Sixteen percent of bird species  
385 (Ottenburghs *et al.* 2015), 6% of European mammals and at least 25% of vascular  
386 plants (Mallet 2005) are thought to hybridise. Ravinet *et al.*, (2018) investigated  
387 signatures of divergence and introgression in a species pair: The Pacific Ocean  
388 three-spined stickleback (*Gasterosteus aculeatus*) and the Japan Sea stickleback  
389 (*G. nipponicus*). These are well-recognised as different species that have sympatric  
390 distributions and crosses showing male hybrid sterility (Kitano, Mori and Peichel,  
391 2007). However, despite the high differentiation, relatively large divergence time  
392 (0.68 – 1 mya) and hybrid sterility, ongoing gene-flow and localised introgression  
393 could nonetheless be detected (maintained in small regions within the genome).  
394 Although the authors are not making a new species claim, this observation of  
395 introgression despite the considerable divergence time is highly relevant to the  
396 speciation question.

397

398 This situation provides challenges for both the PSC and the BSC. How infrequent  
399 do hybridization events have to occur before we consider two biological entities  
400 to be different species? Does it make a difference if such hybridization is sex-  
401 biased? How does regional variation in hybridization rates influence this  
402 inference? The BSC currently has no answer to these questions. Likewise, for the  
403 PSC, “fixed heritable differences” will be immediately mixed in hybrid individuals.  
404 Therefore, temporal or spatial variation in hybridization could lead to transient or  
405 spatially varying species classifications.

406

407 Due to the increasing recognition of the pervasiveness of hybridization and  
408 introgression among recognised species, they are becoming important  
409 phenomena to consider when making taxonomic decisions. The idea that  
410 hybridization may play an important role in evolution was initially explored by  
411 botanists and appears to be particularly important for plants, with approximately  
412 10% of plant species thought to hybridize (Yakimowski and Rieseberg, 2014).  
413 Hybridization is also particularly common in invasive species (Ellstrand and  
414 Schierenbeck, 2000), likely due to hybridization allowing adaptive introgression  
415 of beneficial traits between the taxa (Martin, Bouck and Arnold, 2005, 2006).

416 However, widespread hybridization is not limited to plants and has played an  
417 important role in the adaptive radiation of *e.g.* Heliconius butterflies  
418 (Dasmahapatra *et al.*, 2012). These butterflies are of particular interest in  
419 speciation research because of their huge diversity, with varying rates of  
420 hybridization (Van Belleghem *et al.*, 2017). Their genomes contain what has  
421 become known as “genomic islands of divergence” (Nadeau *et al.*, 2012). Originally  
422 identified in *Anopheles* mosquitos (Turner, Hahn and Nuzhdin, 2005), the origin  
423 and role of these islands was originally interpreted as regions of selection and  
424 reduced introgression between divergent populations, although it is increasingly  
425 being realised that there are processes other than population divergence that may  
426 lead to these patterns (Cruickshank and Hahn, 2014; Wolf and Ellegren, 2017).

427

428 Hybridization complicates taxonomy when we consider that speciation rates, and  
429 levels of subsequent hybridization vary considerably between taxa. The proposed  
430 new species of Darwin’s finch described above showed transgressive segregation  
431 in bill morphology and was ecologically successful. This ongoing finch radiation is  
432 predominantly based on a behavioural trait (i.e. mate choice). Finches imprint on  
433 features of their parents early in life, and choose mates based on bill size and  
434 shape, and body size and song. The driving force behind the speciation events here  
435 is therefore a complex mating behaviour. While these adaptive traits (at least in  
436 the case of bill dimensions) are correlated with detectable genetic variation, it is  
437 their effect on the behaviour phenotype that is relevant for reproductive isolation  
438 and species designation in these taxa. It seems fair to assume that if the  
439 observational data were available, this situation would be representative for most  
440 taxa with complex mating behaviour. However, this is in stark contrast to many  
441 other taxonomic groups, which can take far longer to develop reproductive  
442 isolation. For example, hybridization in marine invertebrates may be extreme.  
443 One study found hybridization between two cryptic species of sea squirt (*Ciona*  
444 *intestinalis*) with an average synonymous sequence divergence of 14.4% (Roux *et al.*,  
445 2013). Rates of introgression in *Ciona* were relatively low, variable among loci,  
446 and unidirectional, consistent with a situation of multiple genetic  
447 incompatibilities throughout the genome, suggesting that genetic incompatibility  
448 was developing, albeit very slowly. It would be interesting to use genomics to  
449 investigate signatures of selection in these *Ciona* populations, to see the extent to  
450 which adaptation can be detected, and how it reflects the taxonomy.

451

452 Previously, we might have written off these examples of extreme hybridization as  
453 being exceptional, however this explanation is becoming more difficult to abide.  
454 As we can see from the stickleback example above (Ravinet *et al.*, 2018), the  
455 phenomenon is not limited to invertebrates. In fact, whole genome data are  
456 detecting instances of introgression in many species and in unprecedented detail.  
457 For example, most non-African humans have 1-2% Neanderthal ancestry (Green  
458 *et al.*, 2010; Prüfer *et al.*, 2014), and a number of human populations have  
459 Denisovan ancestry that is thought to have adaptive significance for adaptation to  
460 extreme altitude (Reich *et al.*, 2010; Meyer *et al.*, 2012; Prüfer *et al.*, 2014). Such  
461 patterns of introgression are mirrored in non-human primates, with evidence of  
462 multiple occurrences between bonobos and chimpanzees during the past 550,000  
463 years (De Manuel *et al.*, 2016).

464

465 These observations complicate the matter of species delineation, because they  
466 suggest that complete reproductive isolation can be withheld for extremely long  
467 periods of time in some taxa (in the case of *Ciona*, for greater than three million  
468 years of divergence in isolation). It could be argued that this is just the BSC  
469 impartially reflecting the variable speciation rates that occur in nature, however  
470 some taxonomists (e.g. with well-known mammalian groups) clearly find such  
471 observations problematic as these instances do not tend to be reflected  
472 taxonomically (e.g. between brown and polar bears, coyotes and wolves). **Some**  
473 **concepts may regard hybridisation as a “consequence”, while others think of it as**  
474 **a defining characteristic. However, hybridisation does not only complicate species**  
475 **designation for the latter. Hybrids may not initially seem relevant to the PSC, but**  
476 **hybrid zones between two different taxa diagnosed using the PSC would create a**  
477 **gradient of alleles, such that the sampling scheme (across the geographic space as**  
478 **well as the genome) and population comparison chosen would dictate whether**  
479 **taxa would be diagnosed as different. This present a challenge, not only for**  
480 **diagnosing different units, but also for describing what those things are from an**  
481 **ontological point of view.**

482

#### 483 ***ARE THE SPECIES CONCEPTS OPERATIONAL IN THE GENOMIC ERA?***

484

485 There are therefore challenges in operationalizing species concepts, but is this  
486 more the case for some rather than others? And how has genomic data facilitated  
487 operationalisation for each concept? The PSC is easier to test in most cases, and  
488 Groves (2013) argued that “*the PSC offers the only criterion for species recognition*  
489 *that is testable, as a scientific proposition should be.*” However, it might be  
490 questioned in what sense the PSC is testable. And if so, is it the only species  
491 delineation approach that is?

492

493 As argued by Groves (2013), the PSC is “testable”, however when we do this we  
494 must be cautious that we are not engaging in an oversimplification. The  
495 application of a testable threshold does not represent progress if that threshold  
496 does not reflect the label that we are trying to establish. Genetic differentiation  
497 among populations can be greatly influenced by demography, including changes  
498 in population size. Genetic structure has been observed to considerably decrease  
499 among brown bear populations (*Ursus arctos*) in just 1.5 generations (Hagen *et al.*,  
500 2015), and genetic structure substantially increased over only eleven years  
501 (approx. five generations) in Coachella Valley fringe-toed lizards (*Uma inornata*;  
502 Vandergast *et al.*, 2016). These examples are not intended to demonstrate that  
503 speciation does not occur over short time periods, but simply that genetic  
504 divergence and population structure may be highly transient, which many people  
505 would argue should not be the case for speciation. Genomics allows for a huge  
506 increase in the power to detect population structure because of the much larger  
507 number of loci available. This has the effect of enabling the identification of very  
508 fine-scale population genetic structure, and consequently more ‘fixed heritable  
509 differences’ between populations. ‘Splitters’ would presumably interpret this  
510 added genomic information as an increase in power of detecting incipient  
511 speciation, whereas ‘lumpers’ would presumably interpret these as ‘type 1 error’  
512 species. In this regard then whether genomics has revolutionised our ability to  
513 identify new species depends on the species concept being applied. Genomics has

514 also allowed for a huge increase in the power to describe demographic histories  
515 (e.g. Nater *et al.*, 2017), and this information is important to present alongside that  
516 of genetic structure when making a species claim, so that that claim can be  
517 assessed in its full context.

518

519 All but one of the examples discussed here have used genetic structure as a part  
520 of their evidence, however it is notable that the porpoise (Zhou *et al.*, 2018),  
521 orangutan (Nater *et al.*, 2017) and stickleback (Ravinet *et al.*, 2018) studies also  
522 include demographic analysis, whereas the giraffe study (Fennessy *et al.*, 2016)  
523 did not. Genetic structure does not distinguish between isolation and migration  
524 and so is very difficult to interpret on its own. In addition, the first three studies  
525 above used a methodology and dataset that enabled them to estimate genetic  
526 structure that was representative of the whole genome. As we can see from the  
527 stickleback example (Ravinet *et al.*, 2018), and the discussion on introgression  
528 above, using genetic structure based on a small number of loci can be misleading:  
529 Even species with high genomic divergence may have introgressed regions that  
530 will give a very different perspective of the taxonomy - and even without gene flow  
531 incomplete lineage sorting can generate a high proportion of “wrong” gene trees  
532 (Jarvis *et al.* 2014).

533

534 An understanding of population structure can be important for conservation, but  
535 it is important to understand its limitations. Frankham *et al.*, (2012) argued that  
536 species delineations need to be relevant to the point at which populations  
537 have/have not become reproductively isolated (which is not necessarily related  
538 to genetic structure), in order for them to minimise the risk of inbreeding and  
539 outbreeding depression and maximise the benefits of gene-flow. These arguments  
540 led the authors to recommend that only substantial reproductive isolation be used  
541 to define species (for outbreeding sexual organisms) in conservation. Amato &  
542 Russello (2014) commented on this paper, with their main critique being the  
543 difficulty of operationalising the BSC. Frankham *et al.*, (2014) countered that  
544 reproductive isolation generally arises from adaptation to different environments  
545 and/or outbreeding depression caused by fixed chromosomal differences, both of  
546 which can be detected (albeit requiring a more technically challenging approach  
547 than a structure analysis). They stated that “*Divergence should be protected when  
548 it reflects adaptive differences, but countered when it threatens populations.*” The  
549 authors were therefore arguing that the BSC is a better proxy for adaptive  
550 potential than the PSC. **It is important to note that this argument is predominantly  
551 based on the BSC being a better tool for recognising conservation units, and  
552 therefore is not addressing its ontological relevance. Nonetheless, adaptive  
553 potential is important if we want to conserve populations that are able to adapt to  
554 changes in their environment.** However, is it true that the BSC preserves adaptive  
555 potential better, and if so, are there limits and/or exceptions to this?

556

#### 557 ***WHICH SPECIES CONCEPT BEST CONSERVES ADAPTIVE POTENTIAL?***

558

559 Adaptation to novel ecological opportunities is one of the main drivers of  
560 speciation (Van Belleghem *et al.*, 2017), and predicting the capacity of taxonomic  
561 groupings to respond to changing environments is therefore crucial to their  
562 conservation (Eizaguirre and Baltazar-Soares, 2014). The Darwin’s finch example

563 above is a clear demonstration of the potential of hybridization to produce a  
564 population with unique adaptive potential. However, this hybridization and  
565 introgression may have a confounding influence on species delineations  
566 (particularly for the BSC), which is exacerbated when we also consider the  
567 adaptive advantage that introgressed genes may bring. This process, adaptive  
568 introgression, poses a challenge to the claim that the BSC is a good proxy for  
569 adaptive potential. Even very low levels of introgression can have a large effect on  
570 the adaptive potential of the recipient population; adaptive genetic variation has  
571 the potential to move to high frequencies very quickly in a population (Maynard  
572 Smith and Haigh, 2008). In addition, the adaptive potential of the introgressed  
573 material may vary between the donor and recipient populations, depending on  
574 factors such as population size and selection regime. Therefore, in some  
575 situations, taxa designated by the BSC (even when allowing for very low levels of  
576 introgression) may be reflective of adaptive differences between them (e.g. the  
577 adaptive differences in the Darwin's finch example). However, in many situations  
578 it will not. For example, it seems highly likely that the two distinct populations of  
579 sea squirts (*Ciona*) (Roux *et al.*, 2013) have accumulated considerable adaptive  
580 differentiation in their three million years of divergence in isolation, regardless of  
581 the fact that gene-flow has now been re-established. This gene-flow would  
582 preclude these as separate species under the BSC, and therefore (unlike with the  
583 finches) the taxonomy would not reflect the adaptive differences between  
584 populations/species. Hence, the BSC will better represent adaptive differentiation  
585 in some comparisons than in others, and this may be biased towards taxonomic  
586 groups with particular life-history traits. It should also be noted that this is no less  
587 the case for the PSC. If our goal is to conserve adaptive potential in an unbiased  
588 way across all taxa then this is a crucial point to consider. Many scientists argue  
589 that maximizing phylogenetic diversity will indirectly capture functional diversity  
590 (Vane-Wright *et al.*, 1991; Faith 1992; Winter *et al.*, 2013). However, a recent  
591 study by Mazel *et al.*, 2018 has shown that phylogenetic diversity does not reliably  
592 capture functional diversity.

593  
594 This raises the question of why not simply measure adaptive potential directly?  
595 Genomics is starting to allow us to do this. For example, Zhou *et al.*, (2018)  
596 identified evidence of selective sweeps in a number of genomic regions across the  
597 porpoise genome using a method that looks for distinctive patterns of allele  
598 frequencies along a chromosome (Nielsen *et al.*, 2005). Other commonly used  
599 methods for detecting selection include: 1. Identification of extended haplotypes  
600 that are at, or near fixation in a subset of individuals (Sabeti *et al.*, 2007), 2. Outlier  
601 methods that compare a model based on including versus excluding selection (Foll  
602 and Gaggiotti, 2008), 3. Attempts to identify correlations between SNPs and  
603 environmental variables (Coop *et al.*, 2010). In the porpoise example, Zhou *et al.*,  
604 (2018) found regions that have a plausible link to morphological characteristics  
605 that differentiate the two proposed incipient species. Applying these methods has  
606 the benefit of not requiring the assumption that adaptive differences are related  
607 to reproductive isolation or genetic structure, which, as described above, may be  
608 inaccurate. It should be noted however that tracking adaptive changes using  
609 genomics is challenging for many traits, especially those that have low heritability  
610 or are highly polygenic (Hoffmann, Sgrò and Kristensen, 2017). However, it is  
611 often hard to convincingly demonstrate selection on a given region of the genome

612 as in many cases it is only the regions undergoing strong haplotypic selection that  
613 will be detected in the analyses discussed above. Furthermore, demonstrating  
614 past selection may not necessarily be associated with contemporary or future  
615 adaptive potential of a genome/genomic region, given that selection pressures are  
616 dynamic. Finally, even if a genomic region can be identified as being under  
617 selection, determining the specific “cause” of this pressure can be highly  
618 challenging, particularly for non-model organisms.

619

620 We have argued that some species concepts may be more applicable (in terms of  
621 relating to adaptive potential) to some taxa than others. For example,  
622 reproductive isolation may be a useful criterion in the case of Darwin’s finches,  
623 since it aligns with the behavioural, morphological and ecological differences  
624 between populations. For organisms like sea squirts, genetic distance and  
625 differentiation may be a better reflection of the differences that have accumulated  
626 over long periods of temporal and spatial isolation. The relationship between  
627 adaptive potential and species concept therefore seems to depend on the taxa  
628 being investigated. This does not necessarily mean that these are not good criteria,  
629 independently, for defining species. However, it certainly complicates  
630 conservation strategies that aim to maximise evolutionary potential, especially  
631 when only one is considered at a time. We would therefore caution against  
632 focusing on a single species concept, especially when the taxa in question are of  
633 conservation concern. In this situation it is important to be very clear about which  
634 concepts are being invoked, and how the evidence presented supports them. **It is**  
635 **important to incorporate multiple lines of evidence into taxonomic decisions**  
636 **(which is increasingly being done; Schlick-Steiner et al. 2010) however,** this  
637 evidence can now theoretically be provided by entirely by genomics: 1.  
638 Morphological evidence can be identified via differentiation in developmental and  
639 structural genes, 2. Biogeographic evidence can be provided using sophisticated  
640 genome-scale modelling, 3. Behavioural differences can be inferred by identifying  
641 genes associated with behaviour, mate-choice, and also by detecting sex-biased  
642 demography, 4. Ecological evidence is available in the form of genomic signatures  
643 of selection to environmental factors, 5. Reproductive compatibility can be  
644 observed as sex chromosome compatibility/incompatibility, chromosomal  
645 structure, and epigenomic transmission. In lieu of a definitive conclusion as to the  
646 most appropriate species concept to be used, best practice would be to investigate  
647 as many of the above lines of evidence as possible, and to apportion ones  
648 confidence in a species designation based on the combined weight of all of them.  
649 Recently, Kitchener et al (2017) introduced the concept of a ‘traffic light’ system  
650 for evaluating the strength of evidence of the above 5 categories of species  
651 differentiation, which may provide a pragmatic approach to evaluating genomic  
652 data in specific definition if applied sensibly.

653

654 One thing that both ‘splitters’ and ‘lumpers’ seem to agree on is that it is preferable  
655 that conservation decisions are based on sound scientific evidence. Any ‘planning  
656 blight’ due to taxonomic uncertainty can be detrimental to conservation, and  
657 renders decisive action more difficult. However, while we still have some way to  
658 go before genomic techniques reach their full potential as a diagnostic tool for  
659 species delineation, if the ultimate goal of conservation is to preserve adaptive  
660 potential, genomics is now allowing us to gain a better understanding of this in

661 wild populations. A pragmatic approach could be to use genomic tools to  
662 characterise adaptive potential regardless of the species concept, or even without  
663 invoking a species concept at all. However, answering the question of whether and  
664 to what extent such studies *should* focus on adaptive potential is a separate  
665 challenge.

666

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668

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671

672

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