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

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

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

Recently, Gippoliti *et al.*, (2017) describe the opposing argument that 'taxonomic inertia' is actually more detrimental to conservation, highlighting the case of African ungulates. They argue that the history of African ungulate taxonomic classification has been dominated by 'lumpers' who, when faced with difficult taxonomic decisions, have avoided the situation by assigning a large number of subspecies or genetic lineage labels. According to the authors, this has led to a disproportionately small number of ungulate species being recognised in Africa (despite Africa being by far the leading continent in terms of recognized ungulate species richness (Heywood 2010)). Key to the argument of Gippoliti et al. (2017) is a survey by Morrison *et al.*, (2009), which showed that taxonomic splitting has a positive effect on conservation. Morrison *et al.*, (2009) identify numerous situations where a change in taxonomy has led to increased conservation efforts. One representative example is the California gnatcatcher, *Polioptila californica*. Morrison *et al.,* (2009) highlight the increase in conservation funding (better habitat protection and monitoring programs) that this species received after recognition of its species status. However, a change in protection (conservation) 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 (Ne), and may be very short if Ne 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
Newly proposed species				
Giraffe	Fennessy et al (2016)	One draft genome	• Phylogeny • Genetic structure (Using 7 intron loci and mitochondrial DNA)	Unique genetic character states (PSC)
Orang-utan	Nater et al. (2017)	37 resequenced genomes	• Phylogeny • Genetic structure • Demographic history • Morphology (Genetic data from two, and morphological data from one *Pongo tapanulienis* individual[s])	Unique genetic and morphological character states (PSC)
Finless porpoise	Zhou et al (2018)	48 resequenced genomes	• Phylogeny • Genetic structure • Demographic history • Signatures of selection	Reproductive isolation (BSC)
Darwin's finch spp.	Lamichhaney et al (2017)	47 resequenced genomes, genomic data from 180 individuals from previous study	• Phylogeny • Morphology • Pedigree assessments • Demographic history • Phenotype-genotype associations •	Reproductive isolation (BSC)
Currently recognised species				
Stickleback spp.	Ravinet et al (2018)	27 resequenced genomes	• Phylogeny • Demographic history • Detection of introgression • Genetic structure • Signatures of selection	Species claim not made in this study, but well-recognised as different species with reproductive isolation, and ecological and phenotypic differences (BSC)

209
210 ***NEWLY PROPOSED SPECIES***
211

212 *Giraffe*

213 Recently, Fennessey *et al.,* (2016), produced a draft genome for the giraffe (*Giraffa*
214 *camelopardelis*), 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*
241   *al.,* (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.

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-
296 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.

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.

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

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

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

Darwin's finches

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

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

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).

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).

THE ROLE OF HYBRIDISATION IN SPECIES DESIGNATION

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.

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.

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).

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

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

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

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 be 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

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

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