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NEWS AND COMMENTARY

Empiricist's view of homoploid hybrid speciation

Is homoploid hybrid speciation that rare? An empiricist's view

G Nieto Feliner, I Álvarez, J Fuertes-Aguilar, M Heuertz, I Marques, F Moharrek, R Piñeiro, R Riina,
JA Rosselló, PS Soltis and I Villa-Machío

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Natural hybridization and its role in evolution and specifically in generating new diversity is an old and yet endlessly revitalized topic (Lotsy, 1916; Anderson, 1949; Stebbins, 1959; Rieseberg *et al.*, 2003; Mallet, 2007; Soltis and Soltis, 2009; Larsen *et al.*, 2010; Arnold *et al.*, 2012b; Pereira *et al.*, 2014; Grant and Grant, 2015; Abbott *et al.*, 2016; Pennisi, 2016). Homoploid hybrid speciation (HHS) is the formation of a new—hybrid—species, independent from its parents, via hybridization with no whole-genome duplication and thus no increase in ploidy. Beyond this basic definition, complete agreement is lacking on key aspects of the process, such as the relative proportions of each parental genome present in a hybrid species, the mechanisms leading to reproductive isolation (RI), the degree of RI or the role played by hybridization in the process (Rieseberg, 1997; Abbott *et al.*, 2010). While our understanding of HHS has been improved by detailed evolutionary case studies documented by recent reviews (Abbott *et al.*, 2013; Yakimowski and Rieseberg, 2014; Payseur and Rieseberg, 2016) and empirical studies focused on mechanisms leading to HHS (Renaut *et al.*, 2014; Selz *et al.*, 2014; Lukhtanov *et al.*, 2015), there is controversy concerning the criteria to identify and demonstrate HHS, and even the range of situations that HHS might encompass.

For more than two decades, phylogenetic studies have reported the discovery of putative hybrid lineages at a continuous pace (for example, Rieseberg and Soltis, 1991; Rieseberg *et al.*, 1996; Soltis and Soltis, 2009; Blanco-Pastor *et al.*, 2012; Sousa *et al.*, 2016). In parallel, and partly to sort out the wealth of reported cases, attempts have been made to distinguish among those case studies that convincingly demonstrate HHS from those that correspond to other evolutionary contributions of hybridization or gene flow, for example, adaptive introgression (Rieseberg, 1997; Gross and Rieseberg, 2005). But HHS and such other evolutionary contributions of hybridization lie along a continuum, and in fact adaptive introgression may be involved in HHS (Seehausen, 2004,2013; Abbott *et al.*, 2013). Therefore, focusing our discussion just on HHS is a simplification if one is interested in understanding the role of hybridization (without polyploidy) in differentiation and speciation. However, the HHS concept is widely used, and we think that pointing out potential weaknesses in criteria that are too stringent is useful to avoid misconceptions and contribute to a solid and, at the same time, open conceptual framework (Wiens, 2004) for such a complex topic.

Yakimowski and Rieseberg (2014) list 19 putative cases of HHS among seed plants, two of them in genera in which more than one species is of hybrid origin. Previously, Gross and Rieseberg (2005) considered nine additional cases, including four invertebrates and one fish, and Abbott *et al.* (2013) recognized additional examples among fishes (Stemshorn *et al.*, 2011), sparrows (Elgvin *et al.*, 2011), and butterflies (Kunte *et al.*, 2011). Altogether, there are probably more than 30 cases that have received molecular support as homoploid hybrid species. In contrast, in a recently published paper, Schumer *et al.* (2014) suggested that a putative hybrid species should satisfy three criteria for confident consideration as such. These criteria are: (1) a strong RI mechanism between the putative parental and hybrid species; (2) genetic evidence of hybridization; and (3) isolating mechanisms derived from hybridization itself. They concluded that only four examples across the living world fulfil these three requisites and are thus considered as true homoploid hybrid species: the butterfly *Heliconius heurippa* (Salazar *et al.*, 2010) and the three hybrid sunflower species, *Helianthus anomalus, H. deserticola* and *H. paradoxus* (Rieseberg, 1991).

We think that the views in Schumer *et al.* (2014) illustrate a trend that narrows the concept of HHS, and we question, in this commentary, their concept by examining its pros and cons, for example, of concentrating the discussion of HHS primarily on RI, and discussing whether the importance and frequency of HHS can be assessed under such a position. We believe that the HHS concept remains operationally useful to account for the generation of stable novel diversity via hybridization without polyploidy, provided that it can fit a broader scope of scenarios than those depicted by the above-mentioned stringent criteria.

G Nieto Feliner, I Álvarez, J Fuertes-Aguilar, R Riina, I Villa-Machío are at Real Jardín Botánico, CSIC, Madrid, Spain; M Heuertz is at BioGeCo INRA, Université de Bordeaux, Cestas, France; I Marques is at Department of Agricultural and Environmental Sciences, High Polytechnic School of Huesca, University of Zaragoza, Huesca, Spain; and the UBC Botanical Garden & Centre for Plant Research, University of British Columbia, Vancouver, British Columbia, Canada; F Moharrek is at Department of Plant Biology, Faculty of Biological Sciences, Tarbiat Modares University, Tehran, Iran; R Piñeiro is at Jodrell Laboratory, Royal Botanic Gardens, Kew, Richmond, UK; JA Rosselló is at Jardí Botànic, Universitat de Valencia, Valencia, Spain; PS Soltis is at Florida Museum of Natural History, University of Florida, Gainesville, FL, USA
Correspondence: Dr G Nieto Feliner, Department of Biodiversity and Conservation, Real Jardín Botánico, CSIC, Plaza de Murillo 2, 28014 Madrid, Spain.
E-mail: nieto@rjb.csic.es
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HYBRIDIZATION-DERIVED ISOLATION

Schumer *et al.* (2014) consider that a case fulfils the requirements for being considered HHS if the hybridization event itself was the original trigger of RI. This criterion is based on the argument that the four most compelling cases of hybrid speciation combine genetic evidence of hybridization with evidence that hybridization led to the emergence of RI. We rather believe that the reason why those cases are convincing is that they have been more thoroughly studied in every aspect, not only the origin of RI but also the contribution of hybridization to ecological divergence (Rieseberg *et al.*, 2003) and how quickly hybrid genomes stabilize (Buerkle and Rieseberg, 2008), among other topics. Furthermore, we think that if there is evidence that a hybridization event has given rise to an established, persistent, morphologically and ecologically distinct hybrid lineage, the recognition of this fact should not be compromised by whether or not we can demonstrate that hybridization was directly the cause of RI. Hybridization can be causative of mechanisms that contribute to enhancing RI in hybrid lineages, for example, the sorting of chromosomal rearrangements along the recombinational speciation model (Lai *et al.*, 2005; Lukhtanov *et al.*, 2015) or the occurrence of new traits that change mating patterns (Vereecken *et al.*, 2010; Selz *et al.*, 2014; Marques *et al.*, 2016; Ma *et al.*, 2016). In addition, intrinsic changes in the hybrids not directly causing RI between hybrid lineages and their progenitors may ultimately lead to external RI by facilitating the colonization of new niches (Grant, 1981; Gross and Rieseberg, 2005). But the possibility that RI results from geographical and/or ecological barriers that are not traceable to the hybridization event cannot be excluded. *Senecio squalidus*, a hybrid species formed in Great Britain, acquired geographic isolation from its parents, both of which occur on Mount Etna, Sicily, when it was introduced into the UK (James and Abbott, 2005). We fail to see why this case in which hybridization itself is not the direct cause of RI should not be considered a homoploid hybrid species. Creating such eco-geographic barriers between hybrids and parental species need not rely on human-mediated dispersal. Mechanisms acting on small time scales and macrospatial scales, such as long distance dispersal (LDD) of hybrid lineages, may bring about a rapid isolation but gradual mechanisms probably more commonly lead to external RI. For instance, migration and recurrent bottlenecks seem to have isolated *Pinus densata* from its congeners (Wang *et al.*, 2011).

In addition, we argue that requiring hybridization to be the direct cause of RI may shift the focus of the research away from a crucial aspect of HHS: the production of raw genetic material for selection at higher rates than mutation (Grant and Grant, 1994; Arnold *et al.*, 2012a; Abbott *et al.*, 2013), which can be a source of evolutionary novelty (Soltis, 2013; also for allopolyploids, Soltis and Soltis, 2016). Furthermore, enforcing the hybridization-derived RI criterion might also imply uncritically assuming a role for RI in HHS that is pivotal under a specific model of speciation, which fits the biological species concept, but is not considered crucial under others (see below). From an epistemological point of view, establishing a stringent set of criteria for falsifying putative HHS hypotheses could be seen as an advantage, but this is at the cost of establishing an overly restrictive criterion.

The first criterion advocated by Schumer *et al.* (2014) for recognizing true cases of HHS, that of demonstrating strong RI, is not controversial in itself but altogether illustrates our insufficient understanding of the HHS process(es). RI is a *sine qua* non condition to initiate speciation (Coyne and Orr, 2004) and intrinsic reproductive isolating mechanisms, in particular, maintain integrity of species whenever they come into contact. There is much theoretical and empirical research on the components of RI (Lafon-Placette and Köhler, 2016; Pease *et al.*, 2016) and how to identify and measure them (Ramsey *et al.*, 2003; Martin and Willis, 2007; Sobel and Chen, 2014). However, there is also a growing concern about the actual role of intrinsic reproductive isolating mechanisms in the speciation process itself, particularly in allopatric speciation (Wiens, 2004) and specifically on whether they are drivers or merely by-products of divergent evolution (Sætre, 2013). Acknowledging this dilemma leads to rethinking whether RI should be considered the major factor for recognizing HHS. Furthermore, beyond the evidence that speciation can occur with considerable levels of gene flow (Mallet, 2005; Smadja and Butlin, 2011; Feder *et al.*, 2012) and that RI is frequently incomplete between well-established species (Grant and Grant, 2002), there is debate as to whether the (more or less episodic) interruptions of RI may stimulate speciation (Seehausen, 2004, 2013; Sætre, 2013; Lamichhaney *et al.*, 2015).

In sum, we think that an alternative view to the question of whether hybridization generates RI in HHS processes is to ask whether hybridization generates novel diversity which, by various means, becomes reproductively isolated and stabilized in a different niche, even if RI is not complete, as expected throughout most of the speciation process (Lowry and Gould, 2016).

AN EMPIRICIST'S APPROACH TO HHS

Are homoploid hybrid species as rare as the criteria of Schumer *et al.* (2014) imply? This question cannot be answered conclusively at this point, and we also ignore here the proportion of hybridization events that have led to speciation (Abbott *et al.*, 2013), but there are hints that HHS is not particularly rare, at least when putative cases of this process are considered with a less stringent view. In addition to the mentioned four paradigmatic cases recognized by Schumer *et al.* (2014), a number of examples of potential homoploid hybrid species have been confirmed: for example, the Oxford ragwort *Senecio squalidus* (James and Abbott, 2005; Brennan *et al.*, 2012), *Iris nelsonii* (Arnold, 1993; Taylor *et al.*, 2013), *Pinus densata* (Wang *et al.*, 2001; Gao *et al.*, 2012), *Penstemon clevelandii* (Wolfe *et al.*, 1998) and *Paeonia anomala* (Pan *et al.*, 2007). Significantly, there are many other potential examples of homoploid hybrid species detected in phylogenetic analyses, which have not been thoroughly studied but have been tested against incomplete lineage sorting and have some temporal trajectory and niche differentiation with respect to their progenitors. One can currently consider those cases as hybrid lineages, pending further study, but it is important to call attention to them because phylogenetic approaches offer powerful methods for discovering HHS and also provide complementary information for speciation studies, particularly when these follow stringent criteria such as those of Schumer *et al.* (2014).

As in any other scientific field, in speciation studies it is important that data are collected within a solid conceptual framework which, however, should remain open for debate (Wiens, 2004). This is especially so when disparate views exist on how theoretical studies about natural hybridization (Barton and Hewitt, 1985; Barton and Gale, 1993; Harrison, 1993) should affect empirical evidence (Butlin and Ritchie, 2013; Servedio *et al.*, 2013). Under this perspective, it would be more helpful to adopt broader conceptual frameworks for HHS than that of Schumer *et al.* (2014) such as those in Abbott *et al.* (2013) and Mallet (2007).

In addition, because all putative cases of HHS are detected and initially studied by empiricists, it would be impractical to rely on analysis of RI for recognition of homoploid hybrid species and to apply restrictive criteria at this stage. We thus think that viewing empirical evidence more broadly will minimize false negatives and allow for other aspects that are as important as RI. In particular, a dimension that requires consideration equal to that of RI and the traits and genes responsible for it (barrier genes) is the ecological context of the HHS process ideally including the traits and genes related to the occupation of a new niche. Given that we cannot confidently expect general patterns in HHS and that the speciation process is a complex continuum (Lowry and Gould, 2016), we think it is preferable to encourage reporting rather than discouraging putative cases of HHS.

In summary, we agree that case studies should rigorously test the role of RI. However, we believe that the benefits that Schumer *et al.*'s restricted vision of HHS may have in terms of facilitating falsification of putative cases do not outweigh two questionable aspects: requiring that RI derives directly from hybridization, which we deem unnecessary, and focusing exclusively on RI, which may shift the interest away from other crucial elements in HHS, that is, the ecological dimensions of the process and the production of novel diversity.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

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