Hybridisation on coral reefs and the conservation of evolutionary novelty

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Abstract Hybridisation was traditionally considered rare on coral reefs. However, a rapid increase in hybrid studies over the last 20 years has revealed that hybridisation on coral reefs is common and widespread. In this review, we summarise the growing body of evidence arising from studies on stony corals and reef fishes to verify the occurrence of hybridisation, and we examine the influence hybridisation has had on the enormous level of biodiversity present on coral reefs. We discuss the challenges of distinguishing hybridisation from alternative hypotheses (e.g. incomplete lineage sorting). This review also explores the evolutionary consequences of hybridisation, which range from increasing genetic diversity and the production of novel lineages that may outperform the parent species, to reverse speciation and extinction by genetic swamping. Instances of hybridisation can be natural or occur as a result of human impacts (e.g. habitat degradation) and distinguishing between these two very different causal mechanisms is important for management. Currently, the legislative status of hybrids is unclear and hybrids are rarely protected in conservation programs. Failing to adequately manage hybridisation and hybrid lineages may lead to potential losses of evolutionary novelty, declines in phylogenetic diversity or species extinctions. To conserve existing coral reef biodiversity, and the processes that generate biodiversity, conservation policies must be re-defined and instances of hybridisation must be assessed and managed on a case-by-case basis [*Current Zoology* 61 (1): 132–145, 2015].

Keywords Coral Reefs, Stony Corals, Reef Fish, Hybridisation, Evolutionary Novelty, Extinction

1 Introduction

The transfer of genetic variation among lineages is an important evolutionary force in many plants (Grant, 1973; Rieseberg and Wendel, 1993) and animals (Lewontin and Birch, 1966; Dowling and Secor, 1997; Arnold, 1997; Mallet, 2005; Abbott et al., 2013). Despite this, hybridisation is often viewed as threatening the long-term persistence of species through assimilation or outbreeding depression (Frankham et al., 2002) and contributing to species extinction (Levin et al., 1996; Rhymer and Simberloff, 1996). The view that hybridisation threatens the genetic purity of parental species and is a violation of species integrity (Mayr, 1963) is pervasive throughout conservation literature. Furthermore, hybridisation is often considered to be an evolutionary dead end because genetic incompatibilities and combinations make hybrids unfit, sterile or absent (Haldane, 1922; Dobzhansky, 1937; Muller, 1942). For example, across a diverse range of heterogametic animals (Schilthuizen et al., 2011) and some dioecious plants (Brothers et al., 2010) the hybrids resulting from heterogametic sex are unfit or sterile (Haldane's Rule -

Haldane, 1922). The concern about the negative affect of hybridisation on biodiversity is warranted in cases where the persistence of native species is threatened by hybridisation with introduced species (Rhymer and Simberloff, 1996; Echelle and Echelle, 1997; Huxel, 1999; Perry et al., 2002). Hence, the threat of genetic assimilation has led to conservation resources being directed away from hybrids and towards the protection of populations that represent distinct evolutionary lineages (Stuart and Parham, 2007; Parham et al., 2001; Stuart and Thorbjarnarson, 2003; Parham et al., 2004).

Hybridisation can also however, have positive effects and increase biodiversity. For example, hybridisation can produce unique genotypes with new adaptive traits allowing the colonisation of new habitats (Martinsen et al., 2001), especially after disturbance (Rieseberg et al., 2003; Riginos and Cunningham, 2007). The introgression of novel alleles or a mosaic of morphological characters can lead to novel adult morphologies and further promote speciation (Dowling and Secor, 1997; Willis, 1997) or increase genetic diversity resulting in fitness benefits or adaptability (Stebbins, 1959; Lewontin and Birch, 1966). Introgressive hybridisation can also faci-

litate ecological partitioning (van Herwerden et al., 2006); enable the colonisation of new habitat, and/or facilitate adaptation to environmental changes (Lewontin and Birch, 1966; Willis et al., 2006; van Oppen and Gates, 2006).

Coral reefs are renowned highly diverse ecosystems (Knowlton et al., 2010), but the mechanisms underpinning the diversifications we see today are not well understood. It was traditionally assumed that the lack of hybrids reported on coral reefs meant hybridisation has not played a significant role in generating diversity (Hubbs, 1955), with some recent studies also suggesting hybridisation is a relatively infrequent event (Vollmer and Palumbi, 2002; Flot et al., 2011; Wei et al., 2012). However, research on hybridisation in the marine environment has lagged behind terrestrial and freshwater systems and a growing body of marine hybridisation research over the last two decades calls for a re-evaluation of the role hybridisation plays in generating coral reef diversity because it is now evident that hybridisation is widespread among coral reef taxa (Veron, 1995; Gardner, 1997; Yaakub et al., 2006; Arnold and Fogarty, 2009; Sanders et al., 2013). The question now is: how has this widespread hybridisation influenced biodiversity on coral reefs?

Understanding how evolutionary processes, such as hybridisation, have generated and shaped the biodiversity of modern coral reefs is crucial to conserving this biodiversity. The global decline of coral reef habitat (Hughes et al., 2003; Pandolfi et al., 2003; Wilkinson, 2004; Bruno and Selig, 2007) has led to declines in the accretion potential and productivity of reefs (Hoegh-Guldbeg et al., 2007). The declining condition of coral reef ecosystems and the increasing multitude of impacts imposed by anthropogenic impacts and rapid global climate change (Hoegh-Guldberg, 1999; Hansen et al., 2013) has resulted in one third of reef-building coral species facing an elevated level of extinction this century (Carpenter et al., 2008) and a growing number of reef fishes at risk of extinction (Zgliczynski et al., 2013). Securing the health and resilience of coral reef ecosystems is imperative, not only because of their diversity and unique geological structure (Kleypas et al., 2001), but also because of their socio-economic value (Moberg and Folke, 1999; Access Economics, 2008). Therefore, as the number and intensity of threats to the biodiversity and resilience of coral reef ecosystems escalates, there is an urgent need to understand the evolutionary processes that generate and maintain coral reef biodiversity (Willis et al., 2006).

In this paper we explore the extent of hybridisation in coral reef ecosystems, by examining reef-building hard corals and coral reef fishes. Both these groups are relatively well-studied and their importance lies in that hard corals are the critical habitat forming organisms in this ecosystem and they support thousands of reef fish species, which form the highest diversity vertebrate communities on Earth (Jones et al., 2002). We examine the potential range of evolutionary outcomes of hybridisation from genetic swamping to the generation of novel lineages. Lastly, we discuss the importance of evolutionary novelty in a changing marine environment and argue that conservation policies must be re-defined in order to protect the inherent processes that drive the generation of diversity.

2   Evidence of Hybridisation in Hermatypic Corals

Among reef-building hard corals, reticulate evolution has played an important role in diversification of the numerous genera including *Acropora*, *Montipora*, *Montastraea* and *Platygyra* (van Oppen et al., 2000; Vollmer and Palumbi, 2002; Richards et al., 2008; Fogarty et al., 2012). Furthermore, it has been hypothesised that rare and endemic Indo-Pacific coral species and putative subspecies may be morphologically unique hybrids (Veron, 1995). Among reef building hard corals, reproductive studies (Willis et al., 1997; Hatta et al., 1999; Willis et al., 2006; Fogarty et al., 2012; Isomura et al., 2013); allele sharing (Hatta et al., 1999; Ordrico and Miller, 1997; van Oppen et al., 2000, 2001, 2002, Volmer and Palumbi, 2002; Richards et al., 2013), polyphyly (Richards et al., 2008; 2013; Huang et al., 2009); 100% observed heterozygosity (Richards and van Oppen, 2012) and chromosomal data (Kenyon, 1997) support the hypothesis that hybridisation is widespread and an important evolutionary process. However the only accepted naturally hybridising coral system is the Caribbean acroporids. The Caribbean system comprises two species *Acropora cervicornis* (staghorn coral, Lamarck, 1816) and *A. palmata* (elkhorn coral, Lamarck, 1816) which hybridise to form a third lineage with intermediate morphology named *A. prolifera* (fused staghorn, Lamarck, 1916). The low species complexity of the Caribbean *Acropora* fauna provides a useful model for unravelling evolutionary relationships and testing the extent and directionality of introgression.

Acropora prolifera was first recognized as a hybrid when molecular analysis showed all individuals examined were heterozygous at three diagnostic nuclear

loci (i.e., *PaxC, miniC, Calmodulin*), which is consistent with them being first generation hybrids (van Oppen et al., 2000; Vollmer and Palumbi, 2002). However because no second generation hybrids (F2) were detected in the *A. prolifera* samples examined, Vollmer and Palumbi (2002) concluded that *A. prolifera* hybrids are "immortal mules" that persist only through asexual fragmentation. If hybrids exist via asexual fragmentation, they would be expected to have very low genotypic diversity, but when the genotypic diversity of *A. prolifera* was examined, it was found to be highly variable; moreover, most of the hybrid individuals had unique genotypes suggesting they were derived from sexual reproduction (Fogarty, 2010). The observed diversity of these individuals was presumed to be related to them having arisen via backcrossing (Miller and van Oppen, 2003). Upon further examination of mitochondrial genes; unidirectional backcrossing was confirmed with *A. palmata* (Palumbi et al., 2012). The current understanding is that *A. prolifera* hybrids can be produced from both *A. cervicornis* and *A. palmata* eggs, but genes flow unidirectionally from *A. palmata* into *A. cervicornis* (Vollmer and Palumbi, 2002; Vollmer and Palumbi, 2006).

In the wider Indo-Pacific *Acropora* community, even though hybridisation is thought to have been an important factor in their evolutionary success (Willis et al., 2006) there are few unambiguous examples of hybrids or hybrid species. This is largely because the identifica-tion of both hybrids and parental lineages is compli-cated by high species diversity (Fig. 1A) and environ-mentally driven phenotypic variation (Fig. 1B, C). Morphology conceals cryptic evolutionary relationships in the genus *Acropora* (Ladner and Palumbi, 2012; Ri-chards et al., 2013), thus genetic identification of spe-cies is complicated when they are recently diverged (e.g. Sáez et al., 2003), when individual species exhibit com-plex meta-population structure (e.g., Pinzón and LaJeu-nesse, 2011) and/or when species are connected through introgression (e.g., Forsman et al., 2009).

Molecular phylogenetic studies on Indo-Pacific acroporid species have regularly found high levels of gene pool sharing, consistent with expectations of ex-tensive introgressive hybridisation and reticulate evolu-tion (Hatta et al., 1999; van Oppen et al., 2000; van Oppen et al., 2002; Richards et al., 2008; Ladner and Palumbi, 2012). However the unknown age of many extant Indo-Pacific species makes it difficult to distin-guish between hybridisation and incomplete lineage sorting (i.e. shared ancestral polymorphism) (van Oppen et al., 2001; Vollmer and Palumbi, 2002; Márquez, 2002; Wolstenholme et al., 2003; Nakajima et al., 2012). In species with large population sizes where lineage sort-ing occurs slowly, ancestral polymorphisms cannot be rigorously excluded as an alternative explanation for polyphyletic patterns. However rare species may pro-vide the opportunity to overcome this problem due to their intrinsically limited population sizes and short

Fig. 1 Morphology conceals cryptic evolutionary relationships in *Acropora* species.
Over 60 species of *Acropora* can occur in sympatry in Indo-Pacific coral communities and the prevalence of phenotypic plasticity greatly compli-cates the identification of hybrid and parental lineages **(A)**. For example, *Acropora clathrata* **(B)** occurs as open branching plates when growing at 5m depth in a sheltered environment (Flying Fish Cove, Christmas Island); and as highly fused plates at 20m depth **(C)** in a high current location (Tom's Point, Christmas Island).

coalescence times. Veron (1995) first suggested that corals with restricted geographic ranges may be morphologically unique hybrids and one study supports this premise (Richards et al., 2008). In this study, nuclear and mitochondrial gene trees were compared to show that numerous species are monophyletic at the mtDNA marker but polyphyletic with highly divergent alleles at the nuclear marker (Fig. 2). Two of the species displaying this pattern have a large global population sizes; however three of them (*A. pichoni*, *A. kimbeensis* and *A. papillare*) are rare; hence they have small effective population sizes (Ne). For these species, unidirectional hybridisation was suggested to be the most parsimonious explanation for their phylogenetic signature. However, if backcrossing is common, and especially if parental lineages are not known, the effective population sizes of rare species may be substantially higher (Stat et al., 2012).

Another putative example of the reticulate evolutionary history of *Acropora* is the finding of a complex syngameon (a group of intermittently interbreeding species) that includes representatives of 10 species derived from 5 different 'species groups' which share identical nuclear alleles (Richards et al., 2013, Fig. 3). In this

syngameon it was proposed that *A. valida* may be acting as a conduit - transferring genetic material between species via introgressive hybridisation. This hypothesis is plausible considering that *A. valida* has a widespread distribution and is phenotypically diverse (Wallace, 1999); it has a multi-allelic profile (Richards and van Oppen, 2012) and chromosomal data suggesting it may be polyploid (Kenyon, 1997). Another study that obtained DNA sequence data from 12 genomic regions shows that two widespread species, *Acropora cytherea* and *A. hyacinthus*, form complexes and a global syngameon with consistent patterns of introgression between species across large geographic distributions (Ladner and Palumbi, 2012).

Acropora rongelapensis (Richards and Wallace, 2004) provides another curious example of a putative hybrid species (Fig. 4a). Microsatellite genotyping conducted on 12 individuals of this species showed heterozygote excess at 6/7 loci and 100% observed heterozygosity (HO) at three loci (Richards and van Oppen, 2012). Fixed heterozygosity may be explained in various ways. First, it could indicate the individuals were produced asexually however no identical MLGs were identified. Second, high heterozygosity may reflect an old, stable,
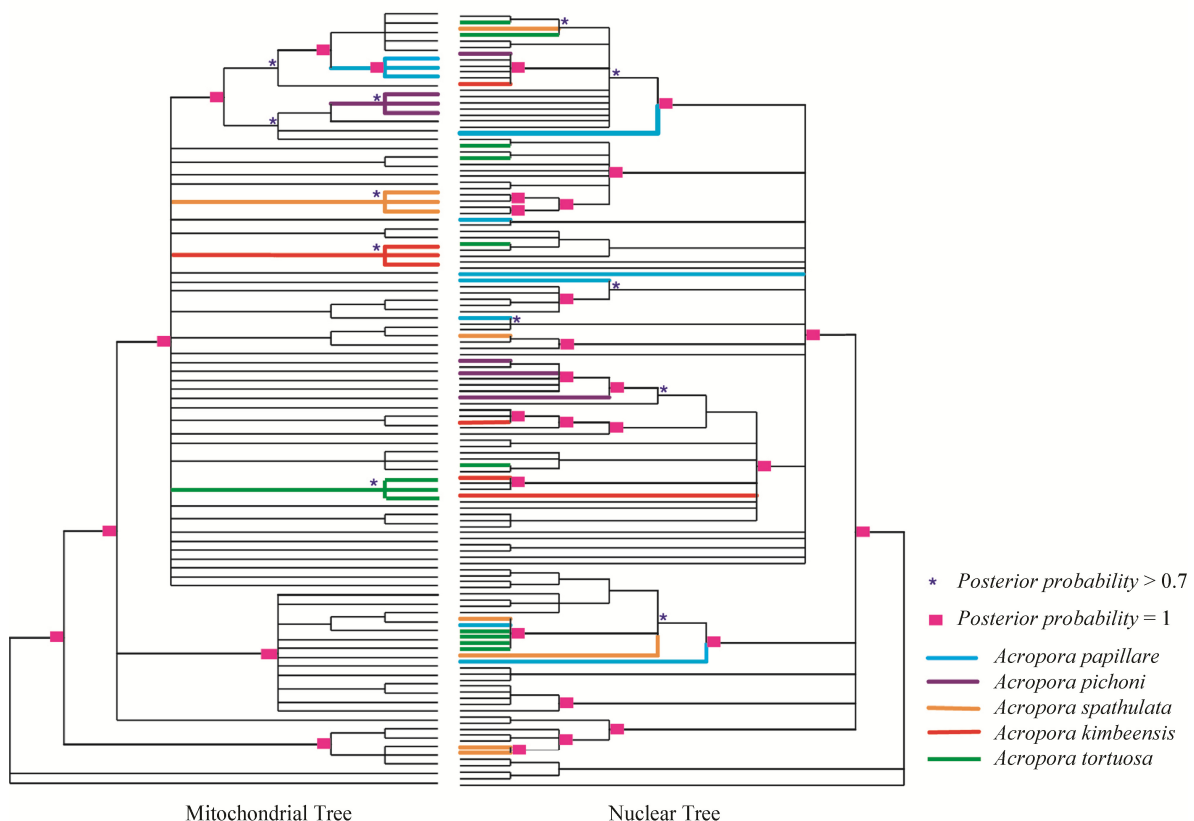

Fig. 2   Comparison of nuclear(*Pax-C*) and mitochondrial (*rns-cox3*) phylogenies.
Posterior probability values are shown only at nodes affecting the positions of sequences from *A. papillare*, *A. pichoni*, *A. kimbeensis*, *A. spathulata* and *A. tortuosa*. (Adapted from Richards et al., 2008).
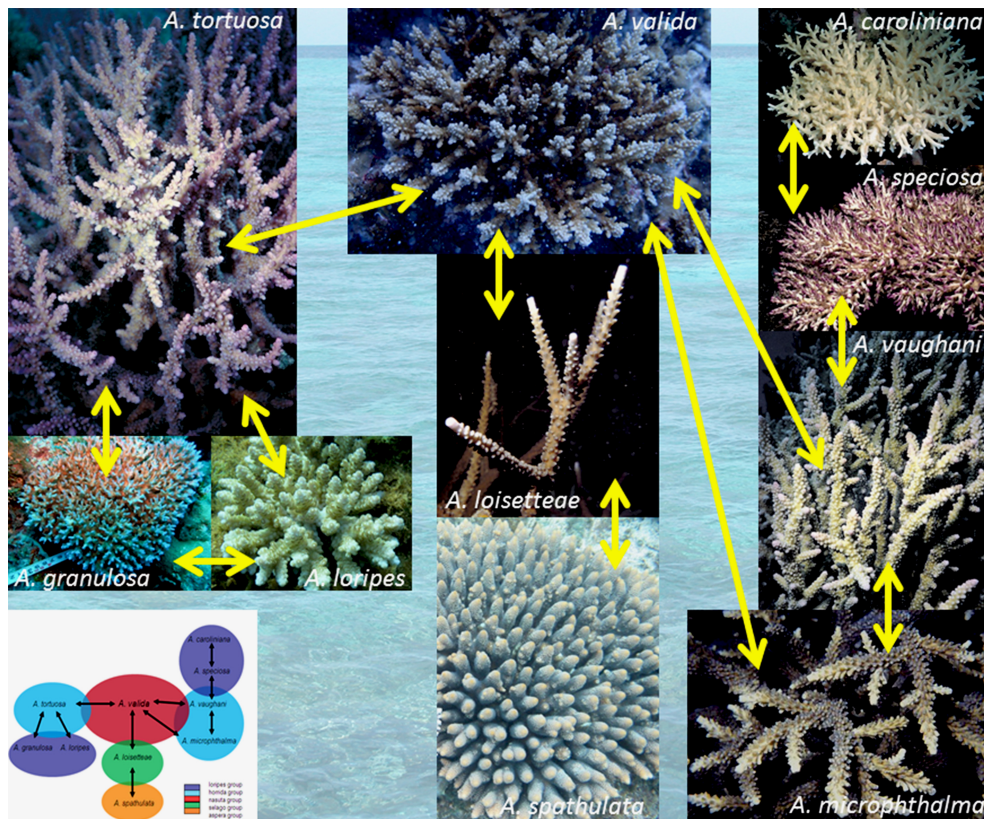
Fig. 3   A complex syngameon representing 10 different Indo-Pacific *Acropora* species that share identical nuclear alleles despite belonging to five different species groups with little apparent phenotypic similarity (Adapted from Richards et al., 2013).

and persistent population or recruits that are derived from various genetically divergent sources (van Herwerden et al., 2009). However, *A. rongelapensis* is a member of the large terminal clade in the *Acropora* phylogeny that is considered relatively young, diverging from its most recent common ancestor at least 5.69 million years ago (Richards et al., 2013) and only a small number of isolated populations of this species have been located across its continuous distribution range (Wallace et al., 2012). Hence, the most likely explanation for the finding of 100% observed heterozygosity in this rare species is that the sampled individuals were F1 hybrids; however to date, the parental lineages have not been established.

In the same population genetic study (Richards and van Oppen, 2012), higher than expected genetic diversity was also detected in *Acropora kimbeensis* which was also found to be monophyletic in mtDNA and polyphyletic in nucDNA (Fig. 2, Richards et al., 2008). Genotyping detected multiple peaks in the chromatogram for a single locus in *A. kimbeensis* and sequencing of cloned microsatellite products verified that more than two alleles were present (Richards and van Oppen, 2012). The finding of gene duplication events lends support to the hypothesis that some rare species are putative hybrids and that introgressive hybridisation boosts
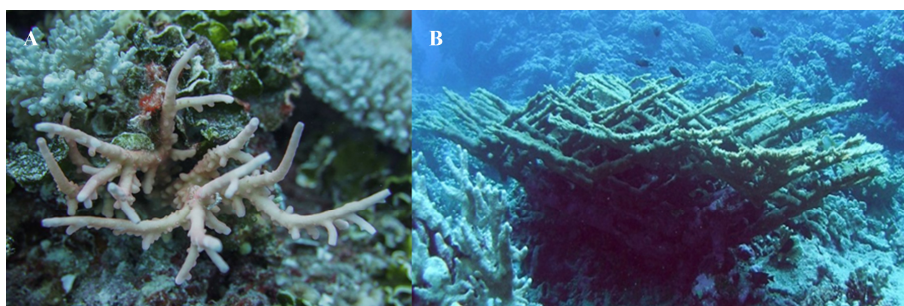

Fig. 4   Putative hybrid coral species.
A. *Acropora rongelapensis*; **B.** *Acropora rotumana*.

genetic diversity in rare species. However, considering multiallelic profiles were not obtained for the other loci, this locus may have undergone a duplication event in this species, rather than this species being polyploid. Alternatively, it could represent a chimeric occurrence as has been demonstrated to occur in other coral species (Puill-Stephan et al., 2009; Work et al., 2011). The possibility that another rare species, *Acropora rotumana* (Gardiner, 1898) (commonly known as the 'Pacific Elkhorn' Fig. 4b) is a polyploid hybrid has also been raised (Richards et al., 2010) but remains to be verified.

3 Evidence of Hybridisation in Reef Fish

A increasing body of evidence shows hybridisation is common and taxonomically widespread among coral reef fishes (Pyle and Randall, 1994; Gardner, 1997; Allen et al., 1998; Mc-Millan et al., 1999; van Herwerden and Doherty, 2006; van Herwerden et al., 2006; Frisch and van Herwerden, 2006; Yaakub et al., 2006, 2007; Marie et al., 2007; Hobbs and Salmond, 2008; Hobbs et al., 2009, 2013; Mullen et al., 2012; Montanari et al

2012, 2014; DiBattista et al., 2012a, b; Coleman et al., 2014; Hobbs and Allen, 2014). At least 83 natural fish hybrids have been reported in the marine environment, involving 132 species across 17 families with hybridisation most-commonly reported among coral reef fishes (Montanari et al., 2012). High rates of hybridisation have been reported for families Chaetodontidae and Pomacanthidae where 25%–30% of species hybridise (Fig. 5; Pyle and Randall, 1994; Allen et al., 1998; Yaakub et al., 2006; Hobbs et al., 2013) and recent molecular research indicates that 55% of species hybridise in the family Siganidae (Kuriiwa et al., 2007). Hybrids have not yet been reported in many other groups of coral reef fishes, including species-rich families such as Apogonidae, Blennidae and Gobiidae (Yaakub et al., 2006). These families tend to be cryptic and have received much less research attention compared to the conspicuously-coloured Chaetodontidae and Pomacanthidae, and therefore differences in hybridisation rates between families may be influenced by differences in detectability and research intensity (Hobbs and Allen, 2014).
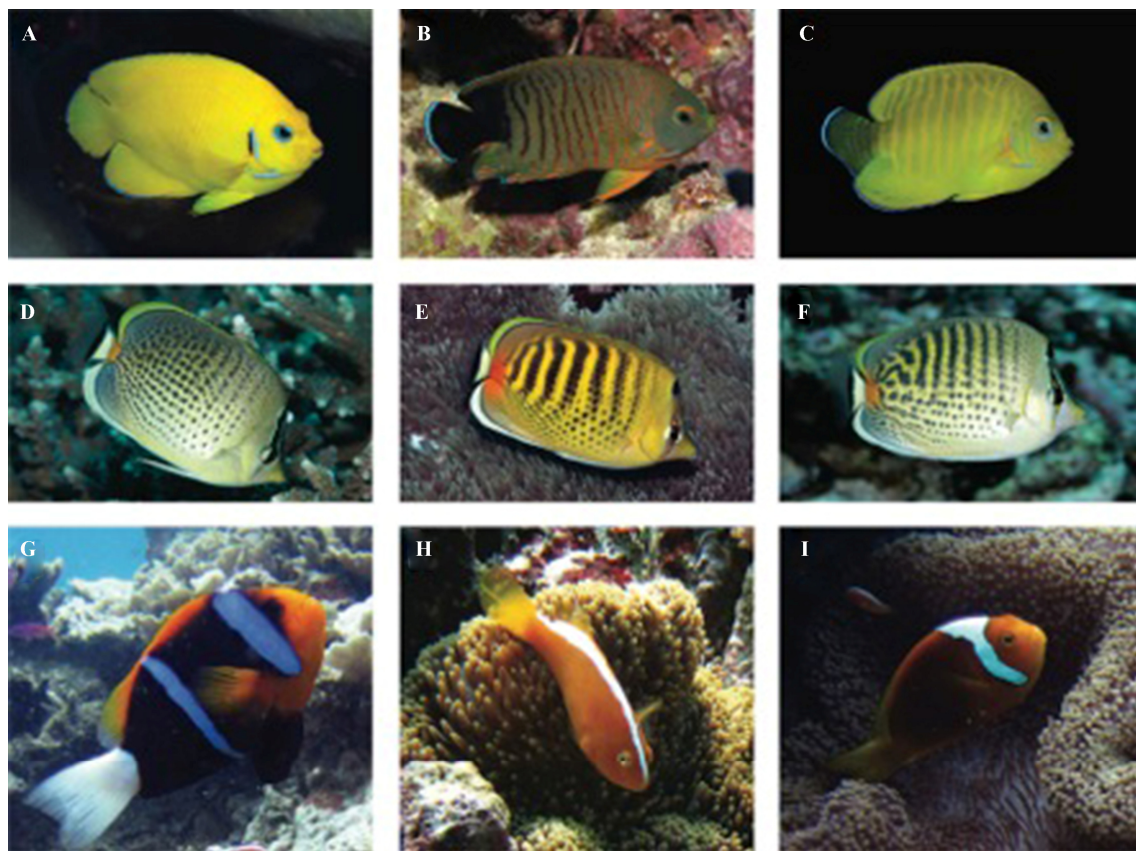

Fig. 5 Hybridisation is a common phenomenon in coral reef fish.
Pygmy angelfish: *Centropyge flavissima* **(A)** and *C. eibli* **(B)** interbreed to produce hybrid **(C)**. Butterflyfish: *Chaetodon guttatissimus* **(D)** and C. *punctatofasciatus* **(E)** interbreed to produce hybrid **(F)**. Anemonefish: *Amphiprion chrysopterus* **(G)** and *A. sandaracinos* **(H)** interbreed to produce hybrid **(I)**, which was previously recognised as the species *A. leucokranos*.

Many hybrid coral reef fishes have been reported based on observations of intermediate colour morphs. Although this does not provide conclusive evidence of hybrid status, recent molecular studies have confirmed that intermediate colour morphs are hybrids across a range of taxonomic groups (McMillan et al., 1999; Yaakub et al., 2006; 2007; Marie et al., 2007; Hobbs et al., 2009, 2013; Montanari et al., 2012; 2014; DiBattista, in review). In addition, there are cases where molecular studies focussed on other topics (e.g. phylogenetics, population genetics) have unintentionally discovered hybridisation and introgression (e.g. Kariiwa et al., 2007; van der Meer et al., 2012), and where long-described species are revealed to be hybrids (e.g. Gainsford et al., in press, Fig. 5). The fact that hybridisation in reef fishes often goes undetected and is more common than first thought is consistent with the pattern of hybrid discoveries in the terrestrial environment (Mallet, 2005). Given that at least 25% of plants and 10% of animals are estimated to hybridise in the terrestrial environment, the high levels of hybridisation (25%–55%) in some reef fish groups (Yaakub et al., 2006; Kuriiwa et al., 2007; Hobbs et al., 2013) indicates that hybridisation on coral reefs is not rare as previously assumed (Hubbs, 1955; Harrison, 1993; Arnold, 1997).

Molecular studies of hybridisation in coral reef fishes demonstrate varying levels of introgression. Hybridisation has facilitated bidirectional gene exchange between some species of reef fishes (Yaakub et al., 2006; van der Meer et al., 2012; Montanari et al., 2014) and unidirectional gene exchange in others (van Herwerden and Doherty 2006; van Herwerden et al., 2006; Montanari et al., 2012). It is not yet clear why some cases of hybridisation only result in gene flow in one direction however possible explanations include differential selection against the different hybrid crosses, mating preferences and abundance of parent species (van Herwerden, and Doherty, 2006; van Herwerden et al., 2006; Frisch and van Herwerden, 2006; Marie et al., 2007; Montanari et al., 2012). In contrast to the above examples, there are some cases of hybridisation among coral reef fishes where there is little or no evidence of introgression (van Herwerden and Doherty, 2006; Yaakub et al., 2007). The reason for the differing levels of introgression among hybridising coral reef fishes has not been fully investigated, but it appears that genetic distance between parent species, abundance of parent species, distribution of habitats and mating preferences may be involved (van Herwerden and Doherty, 2006; van Herwerden et al., 2006; Frisch and van Herwerden, 2006; Yaakub et al.,

2006; 2007; Montanari et al., 2014).

4   Outcomes of Hybridisation

The outcomes of introgressive hybridisation can range from the generation of novel lineages to genetic swamping, which can lead to the evolution of new lineages or reverse speciation, respectively. When introgressed alleles are favoured by selection, low rates of introgression may lead to adaptive shortcuts for the recipient species (Anderson, 1949; Stebbins, 1959). The exchange of novel alleles may provide parental species the opportunity to colonise new habitats or increase their fitness more rapidly than through mutation (Lewontin and Birch, 1966; Dobzansky, 1970; Arnold, 1997). If there is sufficient selection against introgressed alleles, then the ecological and morphological identity of the parental species will be maintained. However, when introgression rates are high as a result of weak selection coupled with extensive hybridisation, the loss of one or both parental species may occur via genetic swamping. Understanding the strength of selection and the reproductive isolating barriers will elucidate the evolutionary trajectory of hybridising species and the likelihood of genetic swamping versus novel lineages.

In situations where backcrossing only occurs with a single maternal lineage this could put the paternal lineage at risk of extinction from genetic swamping. Furthermore, extensive introgressive hybridisation coupled with weak selection against introgressed alleles may result in one species being driven to extinction (unidirectional introgression) or the fusion of species (bidirectional introgression) resulting in the loss of both parental species along with their discrete morphology, behaviour, and ecology (Rhymer and Simberloff, 1996; Levin et al., 1996; Willis et al., 2006). When this occurs, it is often the rarer of the two hybridizing species that suffers increased introgression and is threatened by genetic swamping (Rhymer and Simberloff, 1996; Wirtz, 1999; Levin et al., 1996; Lepais et al., 2009); thus, endangered taxa can be particularly vulnerable.

It is this risk that has caused alarm in the Caribbean system because it was suspected *A. prolifera* was backcrossing only with *A. cervicornis* due to its weak prezygotic barriers and long egg competency times. However recent population genetic research in the Caribbean system suggests the rate of unidirectional introgression varies geographically and among loci and there is natural selection against introgression in some loci (Palumbi et al., 2012). Therefore, differential selection across the

genome of *A. cervicornis* is apparently sufficient to preserve its genetic integrity at key gene regions, despite introgressive hybridisation with its sympatric hybrid partner *A. palmata*. Thus hybridisation does not always produce large-scale introgression. Furthermore, it is expected that with further investigation of *A. prolifera* over a wider geographic area, second-generation hybrids that have arisen via bi-directional backcrossing will be detected (Fogarty, 2012).

Conversely, hybridisation and introgression can have positive outcomes. Hybrid vigour is well established in the plant literature (Fitzpatrick and Shaffer, 2007) and amongst animals there are apparent examples of positive selection for hybridisation (e.g Rosenfield and Kodric-Brown, 2003). In the Caribbean *Acropora* system, hybrids were documented previously as being rarer than the parental species (Goreau, 1959; Lang et al., 1998; Cortes, 2003; Willis et al., 2006). Within the past 5 years, as the parental species have declined the relative abundance of hybrids has increased and hybrid recruits have extended their known range into areas typically dominated by the parental species (Fogarty, 2010, 2012; Japoud et al., 2014). Thus, in this period of coral reef degradation, the Caribbean hybrid *Acropora prolifera* has proliferated and now occurs as a variety of morphologies, in a range of habitats and in both overlapping and distinct communities from the parental lineages. If *A. prolifera* continues to expand its abundance and range, the functional role this species plays in the coral reef ecosystem will increase. Given that stony corals provide food and habitat for a myriad of associated flora and fauna (e.g. fish, crustaceans, molluscs, worms, sponges); an increase in habitat provided by hybrid corals would have flow-on benefits to biodiversity. Hybrids are likely to also provide other important ecosystem services such as reef construction.

Degradation of Caribbean coral reefs also appears to have facilitated conditions conducive to hybridisation in coral reef fish. Habitat partitioning helps separate different species of *Stegastes* damselfish; however, when reef habitats became degraded the different species came into contact and hybridised extensively (Mullen et al., 2012). On degraded reefs, this has resulted in introgression and a blurring of species boundaries (Mullen et al., 2012). In Hawaii, an increase in floating rubbish has facilitated the recent arrival of a vagrant damselfish that have hybridised with an endemic congeneric. Due to introgression, the endemic species is now at risk of local extinction (Coleman et al., 2014). These examples illustrate that, like terrestrial and freshwater systems (Ar-nold, 1997; Rhymer and Simberloff, 1996; Scribner et al., 2000; Seehausen et al., 2008), degradation of environmental conditions appears to promote hybridisation among coral reef organisms. Therefore, reducing anthropogenic impacts on coral reefs to maintain species integrity will further aid in the conservation of coral reef biodiversity.

The above examples from corals and fishes demonstrate that hybridisation can have a range of equally important positive or negative consequences. This reflects the classic scenario of the cichlids in Africa's great lakes where hybridisation was a driver of explosive radiations of species (Seehuasen et al., 2004). However, recent pollution in this system has led to a breakdown in assortitive mating and subsequent hybridisation events have caused reverse speciation (two species become one due to introgression) and thus led to a decrease in biodiversity (Seehausen et al., 2008). While research into the evolutionary consequences of hybridisation is in its infancy for coral reef systems, there is evidence that hybrids can exist as genetic distinct groups (e.g. fish: Montanari et al., 2012; Gainsford et al., in press), and can increase their range and abundance relative to the parent species (e.g. corals: Fogarty 2010, 2012; Japoud et al., 2014). If these hybrids can become reproductively isolated (e.g. through assortitive mating or occupying a niche separate to the parent species) then these hybrid groups could evolve into a new species. There is also evidence that hybridisation has increases genetic diversity of coral reef fishes (van der Meer et al., 2012; Montanari et al., 2014), which may be beneficial to increasing the adaptive capacity of a species. However, there are also instances where natural hybridisation (e.g. van Herwerden et al., 2006; Yaakub et al., 2006; Marie et al., 2007) and hybridisation due to habitat degradation (Mullen et al., 2012; Coleman et al., 2014) appear to be leading to reverse speciation at some locations.

5 Conserving Evolutionary Novelty, Adaptation Potential and the Processes Maintaining Diversity

Current models predict the demise of coral reefs in the next 200 years due to increasing pollution, sea surface temperatures and ocean acidification (Hoegh-Guldberg et al., 2007). It is thus essential to identify habitats, taxa and evolutionary mechanisms that will allow some coral species to maintain their role as foundation fauna for an ecosystem that provides billions of

dollars in services (Hughes et al., 2003; Halpern et al., 2008). Introgressive hybridisation is one mechanism of adaption to changes in environmental conditions (Lewontin and Birch, 1966; Willis et al., 2006; van Oppen and Gates, 2006) which can also result in the evolution of new lineages (Arnold, 1997), and new adaptive radiations (Seehausen, 2004). In as much, hybridisation is an important evolutionary process that must be managed.

Especially among rare species, where the probability of conspecific mating is low, introgression of new alleles into a population may be a critically important source of genetic diversity (Lewonton and Birch, 1966; Grant, 1973; Dowling and Secor, 1997; Seehausen, 2004; Willis et al., 2006; van Oppen and Gates, 2006). However we caution that the finding of high genetic diversity in putative hybrid species may not be functionally informative. This is because most studies examine neutral loci and even if these are found to be genetically diverse, this may not be reflective of the level of diversity in the quantitative trait loci that are under selection in an environmental change scenario (Kellermann et al., 2009; Richards and van Oppen, 2011). We recommend therefore, that in order to better understand the relationship between hybridisation, genetic diversity, adaptive potential and persistence, further robust species-specific genetic diversity estimates at neutral and functional loci are required.

Furthermore, considering environmental selection pressures are important factors in both initiating hybridisation and determining its evolutionary outcomes (Seehausen, 2004; Schluter, 2000; Palumbi et al., 2012), more genetic data are required to ascertain how much of the genome is involved in introgression and to identify which genes are involved in species divergence. If hybridisation leads to polyploidy this would influence a species' ability to evolve because duplicated alleles can evolve freely with little selection pressure which may help organisms adapt to new environments or survive different stress conditions (Comai, 2005). In addition, to further understand the role of hybridisation, reticulate models of evolution (e.g. Linder and Rieseberg, 2004; Gusfield et al., 2004; Huber et al., 2006) must be more widely applied in order to more fully recognize the complex interactions between coral reef species.

6   Redefining Conservation Policy

The ecological and likely evolutionary significance of hybrid corals and reef fishes pose a major challenge to coral reef conservation legislation. Hybrids are currently not considered for threatened species listing and, on this basis, the hybrid coral species *A. prolifera* was explicitly excluded from a recent IUCN Red List assessment (Carpenter et al., 2008). Furthermore NOAA determined that *A. prolifera* did not warrant listing as a threatened species under the US Endangered species Act based upon the false assumption that *A. prolifera* cannot interbreed sexually. It is however, interesting to note that because not all hybridisation events lead to extinction, stable, self-sustaining species of natural hybrid origin are eligible for protection under the US Endangered species Act (Scott, 2006). Nevertheless, because it can be difficult to distinguish between natural and anthropogenic hybridisation and forecast the consequences of hybridisation, it appears that decision makers tend to err on the side of caution, and this is likely to explain why *A. prolifera* and other hybrids are excluded from conservation programs.

We consider avoiding hybrids in coral reef conservation could result in a serious mismatch between policy and real-world conservation needs. Corals from the genus *Acropora* make a case-in-point. Amongst this group of highly threatened corals, putative hybrids are spread right across the web-of-life (Fig. 6); hence failing to protect hybrids could lead to large potential losses of phylogenetic diversity (Faith and Richards, 2012; Huang, 2012). While we do not underestimate the potentially deleterious effects of hybridisation, when hybrids are formed as a result of natural contact between two congeneric populations, a complex variety of ecological and genetic parameters (e.g. vigour and fertility of the hybrids, directionality of backcrossing, the relative and absolute sizes of the hybridising populations, demographic stochasticity and habitat requirements) may influence the risk of extinction of one or both progenitors. Hence, we advocate the most parsimonious approach to the conservation of biotic diversity in coral reef ecosystems has been demonstrated in plant conservation science where the management and protection of hybrid species is considered on a case-by-case basis (van Dyke, 2008).

To date there is no clear predictive framework to assess the likelihood that hybridisation will lead to extinction or the speed at which extinction may occur. Given that hybridisation can be natural or due to anthropogenic impacts, and can have positive and negative consequences (Whitham et al., 1999), there is a need establish a decision framework that includes these causes and consequences to inform case-by-case decisions regarding whether management intervention is justified or not.
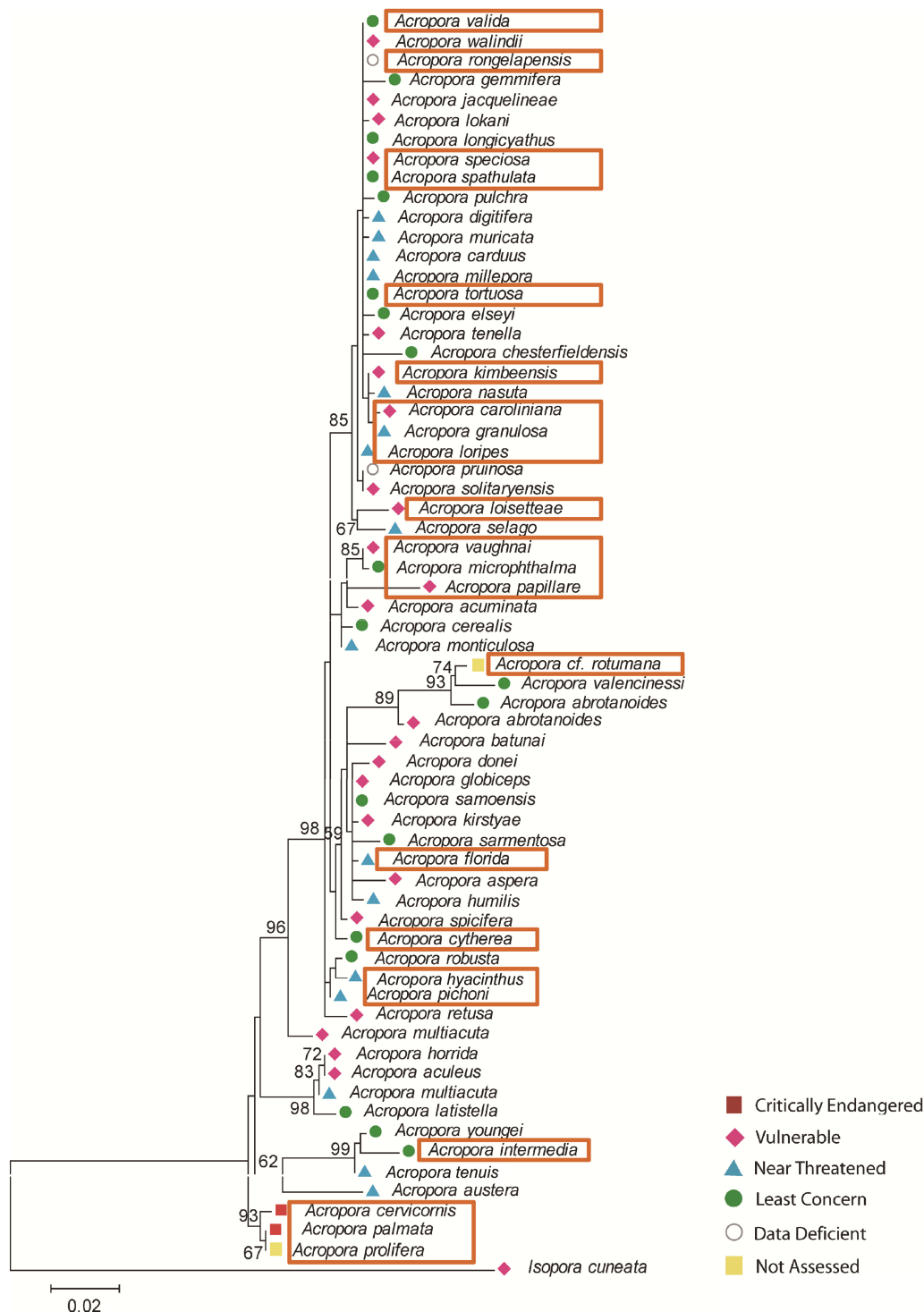
Fig. 6 Putative hybridising species are spread right across the *Acropora* web-of-life

Acropora phylogeny inferred by Maximum likelihood analysis with bootstrap support values indicated next to branches. The IUCN categories are provided for each species and species. Orange boxes are drawn around those species where some evidence has been provided in in peer-reviewed literature to support hybridisation.

Such a decision framework requires theoretical development and would need to include information on (A) the legislative status of the parent species (populations, lineages) and the hybrids. That is, are the parental li-

neages clearly identifiable and genetically distinct? (B) What are the causes of hybridisation (e.g. natural versus anthropogenic) and can they be reversed? (C) The consequences of hybridisation i.e. Is the hybrid of no con-

sequence (unfit/sterile) or could it become reproductively isolated (speciate), or facilitate uni- or bidirectional gene flow? Is introgression occurring at a rate that could lead to genetic swamping and the loss of one or both species? Are the hybrids increasing in abundance? (D) What are the broader implications to biodiversity (e.g. Whitham et al., 1999)? Are any of the species listed or have endangered status? Are there any "pure" populations outside of the hybrid zone? What are the consequences to the rest of the ecosystem if a hybrid increases in abundance? Do hybrids support novel communities, facilitate their speciation and increase biodiversity? Overall, the framework would need to acknowledge that hybridisation can have a range of equally important outcomes, and that preventing extinction due to human-induced hybridisation is just as important as maintaining the potential for natural hybridisation. However, it is inevitable that some situations will present a scientific and ethical dilemma, for example, cases of endangered species that are threatened with extinction due to natural hybridisation.

7 Conclusion

Decision-making processes involving hybridising species require prior information on the causes and consequences of hybridisation. Ecological field studies are important to identifying the causes of hybridisation while molecular studies are necessary to identify the consequences (i.e. the paternal and maternal contributions to hybrid individuals and the level of introgression). There is a need for a more evolutionary process-based approach to conservation (Forest et al., 2007) and species and/or individuals with a putative hybrid ancestry must be considered for protection on a case-by-case basis to maximize the potential for evolutionary novelty. Reconsidering the taxonomic status of hybrid coral and reef fish species is warranted because the current biodiversity conservation legislation may not be compatible with ensuring the biotic diversity of coral reefs or coral reef ecosystem functioning is protected in the long term. Although hybrids may often be viewed as illegitimate offspring and hybridisation considered a threatening process to conserving biodiversity, it can clearly be beneficial in some cases. Thus, it is necessary to broaden our view of the multiple causes and consequences of hybridisation in coral reef ecosystems and to manage specific instances of hybridisation on a case-by-case basis.

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