Title: **The two faces of secondary contact on islands**

Running Title: Secondary contact, heterospecific mating, hybridization, and reproductive interference on islands

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Abstract:
Hybridization is thought to have played an important role in shaping the evolutionary history of diverse island taxa. Here, we propose an ecological and evolutionary framework for understanding the causes and consequences of heterospecific mating on islands – with and without hybridization. There are a number of reasons why secondary contact is expected to be unusually frequent on islands and why heterospecific mating may be a frequent result of such secondary contact. An important contributor is the suite of species and community traits that are enriched by the colonization process itself. The consequences of heterospecific mating may depend, to a large degree, on whether one of the species is introduced. Due to generally weak intrinsic reproductive isolation between island endemics, secondary contact will frequently lead to hybrid establishment and interspecific gene flow. By contrast, due to relatively longer divergence times between endemic and introduced taxa, there will typically be strong

postzygotic isolation between them, and recurrent mating within zones of secondary contact will often lead instead to local exclusion by reproductive interference. Since recent human activity is bringing many insular endemics into contact with introduced relatives, this latter outcome may be an underappreciated conservation threat.

Keywords: island biogeography, colonization, invasive species, hybridization, plant mating systems, genetic swamping, reproductive interference

1. Heterospecific mating on islands

When formerly isolated species come into secondary contact and lack premating isolation, the heterospecific mating interactions that result can have considerable evolutionary consequences. We will refer to such mating events as "hybridization" when interspecific fertilization occurs, and we will refer to viable offspring produced by interspecific fertilization as "hybrids". With or without hybridization, heterospecific mating can substantially affect the evolutionary trajectories of parental species, with a range of outcomes including the reinforcement or breakdown of reproductive barriers (Abbott et al., 2013; Servedio and Noor, 2003; Todesco et al., 2016), homoploid and allopolyploid speciation (Abbott et al., 2013), adaptive radiation (Seehausen, 2004), range expansion (Pfennig et al., 2016), and local exclusion by reproductive interference (Kyogoku, 2020; Kyogoku and Sota, 2017). Although there are a number of exceptional model systems for studying hybridization (Grant and Grant, 2008; Mavárez et al., 2006; Rieseberg et al., 2007), the variety of outcomes that are possible with different combinations of reproductive isolating mechanisms necessitates studying a diversity of systems in order to achieve an understanding of general patterns.

In general, interspecific gene flow now appears to be much more common than historically understood, with evidence of past or ongoing gene flow in at least 10% of animal species and 10-25% of vascular plant species (Mallet, 2005). The recent discovery of hybrid ancestry on many different branches within the tree of life has raised interest in the consequences of interspecific gene flow for long-term taxon survival and functional diversification (Marques et al., 2019; Todesco et al., 2016). Yet, it is equally important to understand what happens when

heterospecific mating fails to result in gene flow – such as when hybrids do not survive to reproduction – and to know how often that happens, although it is inherently more difficult to study (Kyogoku, 2020).

Our objective here is to present an ecological and evolutionary framework for understanding the consequences of heterospecific mating on islands – with and without hybridization. It has long been hypothesized that hybridization occurs frequently between native insular (as pertaining to islands) plant species (Carlquist, 1974) and, with the advent of modern molecular techniques, signatures of interspecific gene flow have been detected in a diverse range of insular taxa (Figure 1). Although differences in regional study effort make reliable comparisons of the frequency of hybrid ancestry between continental and insular environments difficult (Whitney et al., 2010), we propose that islands provide a uniquely attractive setting for disentangling the factors contributing to the divergent outcomes from heterospecific mating. Our first contention is that there are biological reasons to predict secondary contact and subsequent heterospecific mating to be common on islands as a result of their unique eco-evolutionary contexts. Our second contention is that hybrid establishment and interspecific gene flow will be a frequent outcome of heterospecific mating between island endemics as a result of the weak intrinsic reproductive isolation that separates them, whereas negative outcomes, such as local exclusion by reproductive interference (Kyogoku and Sota, 2017), will more commonly result from heterospecific mating between endemic and introduced species due to relatively stronger intrinsic reproductive isolation. We argue that the former may explain the apparent frequency of hybridization on islands, while the latter represents a cryptic and underappreciated threat to native island biodiversity.

Since the prevalence of hybridization on islands appears to be a global trend, we discuss representative examples from several oceanic archipelagos, with a focus predominantly on flowering plants (Figure 1). However, we do not attempt to comprehensively survey hybridization on islands, and so the examples we discuss are selective. Moreover, although our focus is on oceanic islands and archipelagos, many, though not all, of the factors we discuss also apply to other island-like habitats such as lakes, montane sky islands, post-glacial environments, and caves, as well as to the other taxa that inhabit those habitats.
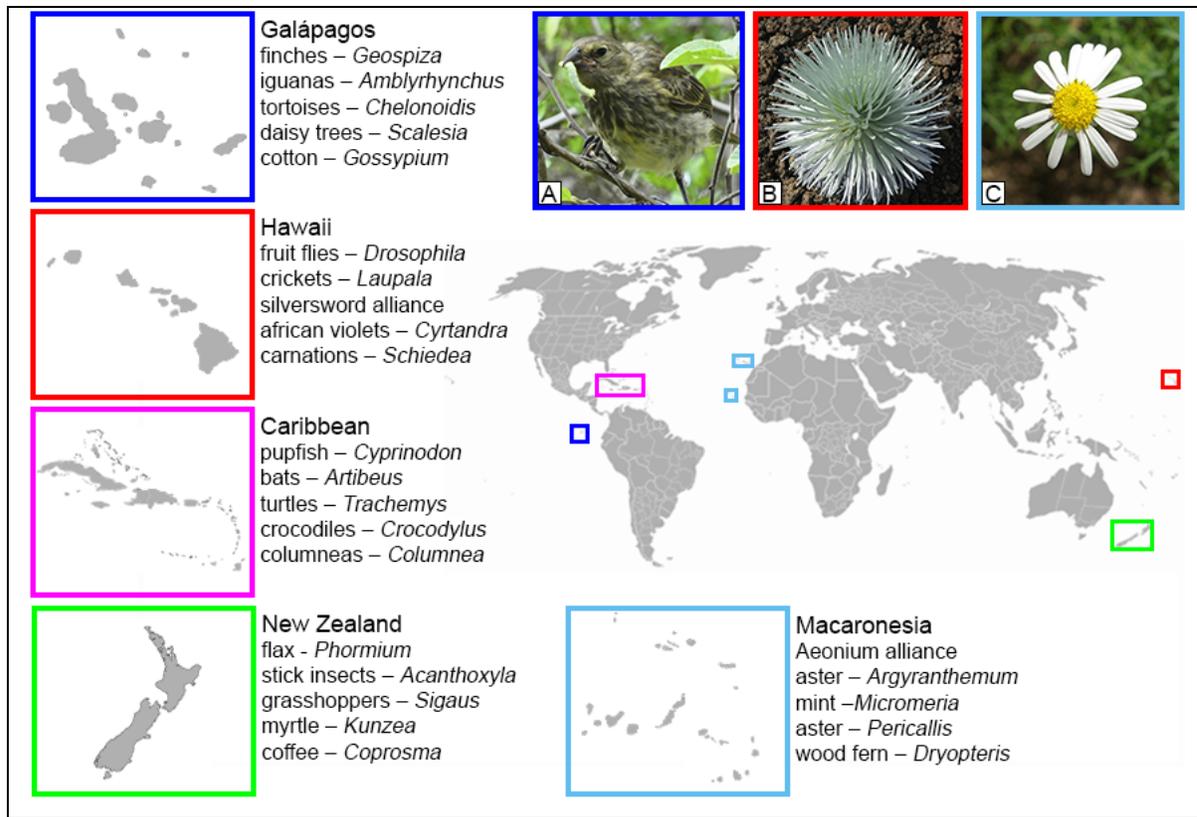
Figure 1. (Left and bottom) Examples of hybridization and introgression from several major oceanic archipelagos discussed in the text, including a number of model systems for studying hybridization (A-C). (A) Finches (*Geospiza*) of the Galápagos have contributed to our understanding of lineage fission via character displacement (Grant and Grant, 2008), lineage fusion via introgressive hybridization (Grant and Grant, 2016), and the first steps of homoploid hybrid speciation (Lamichhaney et al., 2017). (B) The silversword alliance of Hawaii (*Argyroxiphium, Dubautia*, and *Wilkesia*) has been instrumental in our understanding of the development of intrinsic postzygotic isolation in plants (Carr and Kyhos, 1986) and how hybridization can contribute to colonization (Caraway et al., 2001), speciation (Friar et al., 2008), and adaptive radiation (Barrier et al., 1999; García-Verdugo et al., 2013). (C) *Argyranthemum* of the Canary Islands has broadened our understanding of the role hybridization may play in both species collapse (Brochmann, 1984) and speciation (Borgen et al., 2003; Brochmann et al., 2000), with multiple fusion and fission events being observed between the tips of the radiation. Other references by archipelago: Galápagos iguanas (MacLeod et al., 2015; Rassmann K. et al., 2009), tortoises (Garrick et al., 2014; Milinkovitch et al., 2007), daisy trees (Lindhardt et al., 2009; Nielsen et al.,

2003), and cotton (Wendel and Percy, 1990); Hawaiian fruit flies (Brill et al., 2016; Carson et al., 1989; Kaneshiro and Val, 1977), crickets (Shaw, 2002), violets (Smith et al., 1996), and carnations (Wallace et al., 2011); Caribbean pupfish (Richards and Martin, 2017), bats (Larsen et al., 2010), turtles (Parham et al., 2013), crocodiles (Milián-García et al., 2015), and flying goldfish plants (Morley, 1971); New Zealand flax (Houliston et al., 2008; Smissen and Heenan, 2007), stick insects (Buckley et al., 2008), grasshoppers (Dowle et al., 2014), myrtle (de Lange and Norton, 2004), and coffee (Wichman et al., 2002); tree houseleeks (Jorgensen and Olesen, 2001), mint (Puppo et al., 2016), aster (van Hengstum et al., 2012), and wood fern (Gibby, 1985). Image sources: *Argyranthemum,* conservatoire.brest at Wikimedia; silversword, Witort at Wikimedia.

2. The filtering effect of colonization

Islands have unique eco-evolutionary contexts. Many major archipelagos are composed of so called *de novo* islands that have arisen via processes such as volcanic activity (as with Hawaii, Galápagos, and the Macaronesian archipelagos) or changing sea level (as with some Caribbean islands). The emergence times of these terrestrial environments range from millions to tens of millions of years – young relative to continental landmasses (Fernández-Palacios et al., 2011; Neall and Trewick, 2008). The biotas of these archipelagos are the result of geologically recent colonization events followed by *in situ* diversification, leading to mixes of taxa that are nonrepresentative of their continental sources and that include a high proportion of endemics (Kreft et al., 2008; Russell and Kueffer, 2019; Weigelt et al., 2015; Whittaker et al., 2008).
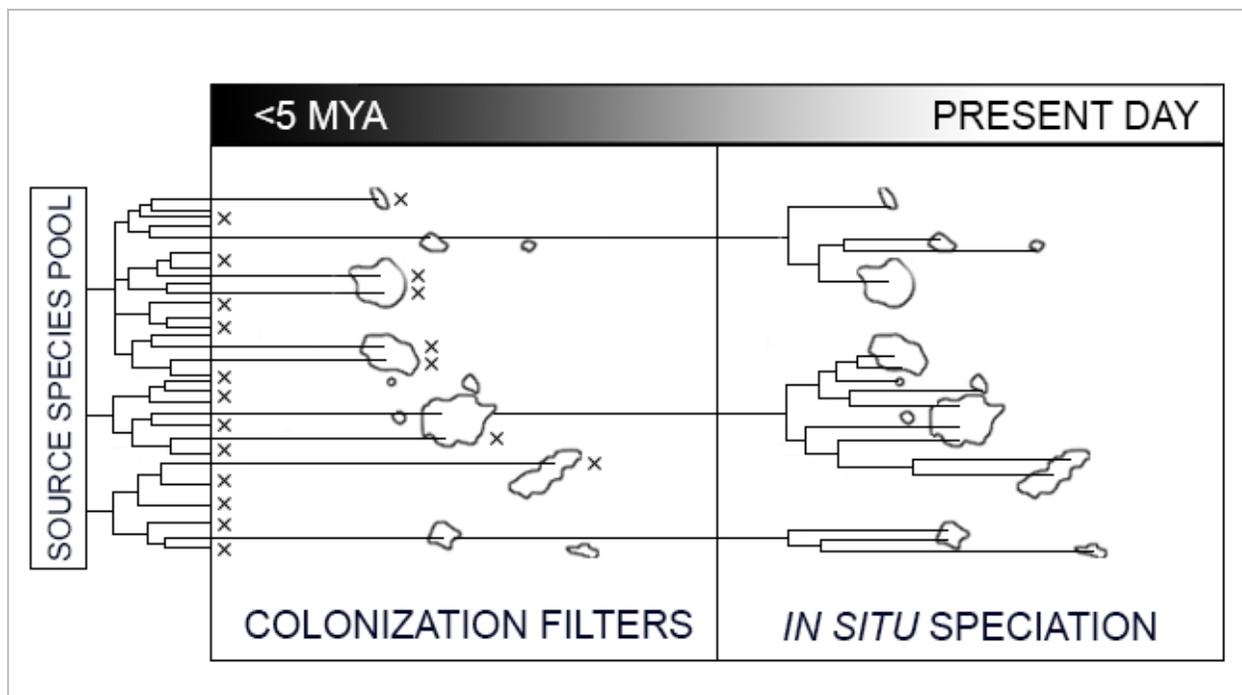
Figure 2. Dispersal and establishment filters during colonization result in unique eco-evolutionary contexts on islands. Successful colonists experience ecological opportunity, which promotes *in situ* diversification and speciation. These endemic clades are young relative to their continental relatives, and as a result species pairs within them generally have weaker postmating reproductive isolation relative to pairs of native and introduced species.

As illustrated in Figure 2, the process of colonization itself functions as a set of filters for taxa possessing traits that aid in establishment and survival within insular ecosystems (Weigelt et al., 2015). The first of these filters is dispersal, the intensity of which depends on island isolation and size (MacArthur and Wilson, 1963; Warren et al., 2015; Weigelt et al., 2015). Successful dispersers then undergo a further environmental filter upon reaching the island, in which species that cannot tolerate the local environmental conditions, and those that cannot survive without community members on which they depend, do not get established (Carvajal-Endara et al., 2017; Weigelt et al., 2015). These filters have four important effects on the species assemblages and ecological conditions of insular ecosystems. First, endemic insular lineages tend to be young as a result of their relatively recent colonization history. Second, niche space on an island may remain unfilled by colonization for an extended period of time, presenting ecological opportunity for those lineages that do successfully establish early (Weigelt et al., 2015; Whittaker et al., 2008).

Third, insular lineages often possess traits associated with colonization such as long-distance dispersal, wide environmental tolerance, and, in some cases, the capacity to reproduce in the absence of conspecifics. Fourth, insular communities are often characterized by generalist species interactions such as, for example, generalist pollination networks for plants (Traveset et al., 2013, 2016).

3. Intrinsic barriers

Might short divergence times within endemic insular clades contribute to a propensity for gene flow between related species on islands? In vertebrates and plants, estimates for the time to achieve complete intrinsic postzygotic isolation – in the form of hybrid sterility or inviability – range from millions to tens of millions of years depending on the taxon (Fitzpatrick, 2004; Levin, 2012; Price and Bouvier, 2002). This not only exceeds the age of many endemic insular lineages, but exceeds the age of many major archipelagos themselves (Fernández-Palacios et al., 2011; Neall and Trewick, 2008). Thus, it is possible that many insular clades are too young for incompatibilities to have accumulated in sufficient number to cause complete infertility and/or inviability. Incomplete intrinsic postzygotic isolation can result in the generation of fertile hybrid offspring capable of backcrossing, which is indeed often posited as an explanation for the observed frequency of hybridization on islands (Crawford and Archibald, 2017). The common occurrence of natural hybrids and evidence for introgression appears to anecdotally support this claim (Figure 1).

A more direct line of evidence comes from experimental crosses, which have been performed in a range of insular plant taxa including Hawaiian *Wikstroemia* (Mayer, 1991), *Labordia* (Motley and Carr, 1998), *Bidens* (Mensch and Gillett, 1972), *Schiedea* and *Alsinidendron* (Weller et al., 2001), *Argyranthemum* from the Canary Islands (Brochmann, 1984), flax (*Phormium*) from New Zealand (Houliston et al., 2008), and daisy trees (*Scalesia*) from the Galápagos (Lindhardt et al., 2009; Nielsen et al., 2003). Fertilization was possible and weak intrinsic postzygotic isolation was found in all of the above cases, although it should be noted that offspring fitness in natural conditions was generally not evaluated.

Perhaps the most robust demonstration of incomplete intrinsic postzygotic reproductive isolation in insular plants has been in the Hawaiian silversword alliance. The maximum age of the alliance is circa 5 million years, which corresponds roughly with the maximum age of the

main Hawaiian Islands (Baldwin and Sanderson, 1998). Crosses have been performed between species that diverged as early as 1 million years ago (MYA) and as late as 5 MYA – including intergeneric crosses with species spanning the three genera of the alliance (*Argyroxiphium*, *Dubautia*, and *Wilkesia*) (Baldwin and Sanderson, 1998; Carr and Kyhos, 1986). A pronounced drop in F1 hybrid pollen fertility is not observed until crosses represent a divergence of at least circa 4.5 MYA, specifically 68% fertility in the cross between *Dubautia sherffiana* and *D. laevigata*. At circa 5 MYA divergence, hybrids between several *Dubautia* species and *Wilkesia gymnoxiphium* had mean fertilities of 28% at the lowest, and the F1 between *Argyroxiphium sandwicense* and *Dubautia menziesii* had mean fertility of 11% (Carr and Kyhos, 1986). Thus, fertile hybrids can be produced even between some of the most divergent lineages of the radiation. Moreover, vigorous bi- and tri-generic hybrids have been produced between mainland tarweeds and silversword allies (Carr et al., 1996).

There do exist counterexamples of strong intrinsic postzygotic isolation between apparently young insular species. There are notable examples in animals, including several pairs of *Anolis* lizards in the Caribbean (Losos, 2009), the iguanas *Canolophus subcristatus* and *Amblyrhynchus cristatus* in the Galápagos (Rassmann K. et al., 2009). In plants, certain young species pairs within the plant genera *Scrophularia* (Dalgaard, 1979; Valtueña et al., 2017) and *Tolpis* (Crawford et al., 2016) in Macaronesia show strong postzygotic isolation. This last example is striking in that hybrids of *Tolpis proustii* and *T. laciniata* in the Canary Islands display low pollen fertilities even though divergence appears to have occurred within only the last million years (Crawford et al., 2016). Nonetheless, these cases appear to be relatively rare.

4. Extrinsic barriers

In the absence of strong intrinsic postzygotic isolation, extrinsic postzygotic barriers, such as ecological selection against hybrids, or extrinsic prezygotic barriers, such as geographic isolation or assortative mating, are likely drivers of speciation on islands (Crawford and Archibald, 2017). However, even these barriers may be relatively weak on islands compared to continental environments as a consequence of their unique ecological contexts and evolutionary histories (Figure 3). We discuss three reasons why such barriers may be weak: (1) disturbance and available niche space may be more prevalent on islands relative to older and more geologically stable continental environments (Figure 3A), (2) island inhabitants are enriched for

long-distance dispersal traits due to their colonization history (Figure 3B), and (3) assortative mating may be frequently compromised on islands, e.g. by generalist pollination networks for plants and by low conspecific mate availability following colonization for all taxa (Figure 3C).
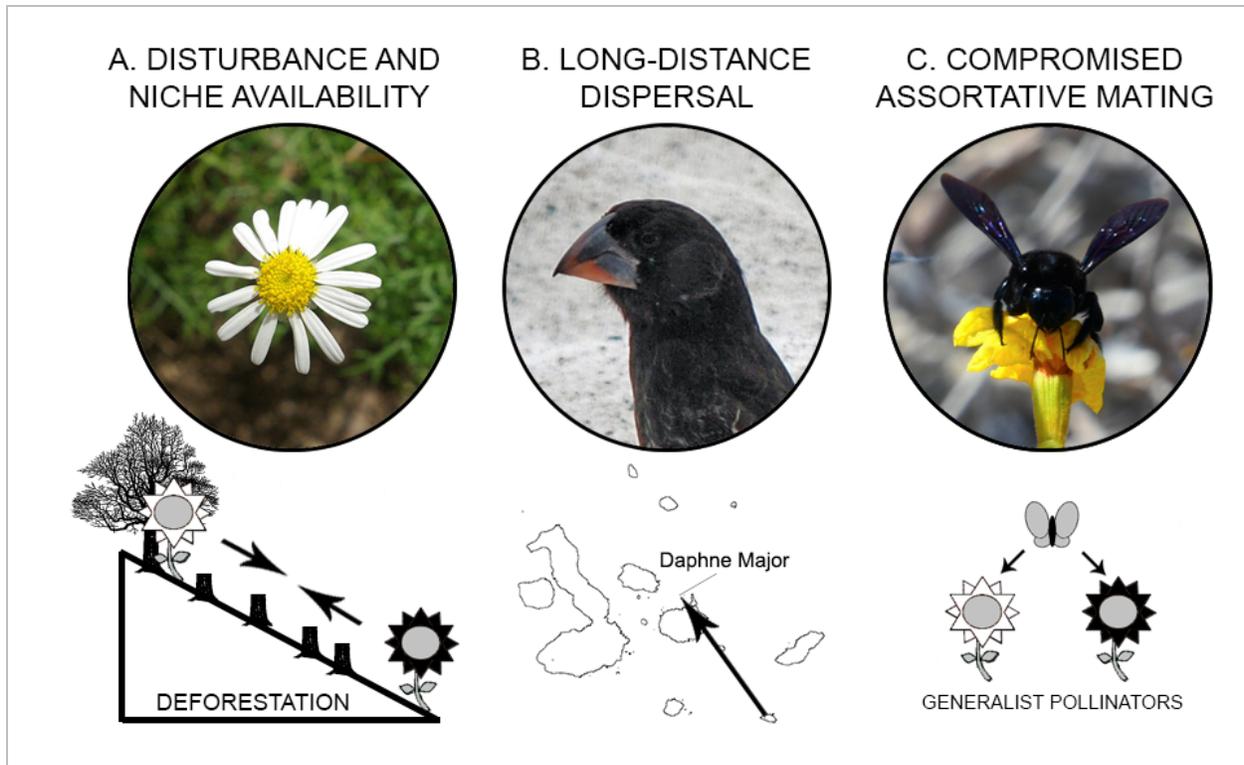
Figure 3. Examples of A) disturbance contributing to secondary contact between montane *Argyranthemum broussonetii* and coastal *A. frutescens* and the establishment of hybrid *A. sundingii* (pictured) in deforested environments in the Canaries, B) long-distance dispersal of a single *Geospiza conirostris* (pictured) individual facilitating secondary contact with resident *G. fortis* and the establishment of an incipient hybrid taxon, and C) compromised assortative mating due to indiscriminate pollination by *Xylocopa darwini* (pictured) of both native and introduced species. Image sources: *Argyranthemum,* conservatoire.brest at Wikimedia; *Geospiza*, Harvey Barrison at Wikimedia.

(a) Ecological opportunity due to disturbance and niche availability

Ecological opportunity, in the form of unoccupied habitats and unexploited resources, may allow the novel genotypes produced by interspecific gene flow to become established with little to no competition from other species (Campbell and Waser, 2001; Ellstrand and Schierenbeck, 2000; Seehausen, 2004). Similarly, habitat disturbance – whether natural or human-mediated –

can facilitate hybridization by resulting in a breakdown of extrinsic reproductive isolation (both pre and postzygotic), and can create suitable habitats for hybrids (Anderson, 1948; Grabenstein and Taylor, 2018; Levin et al., 1996). In general, as the level of ecological instability increases, so too does the opportunity for hybrid establishment and the abundance and diversity of hybrids (Anderson, 1948; Levin et al., 1996).

Islands are non-equilibrium ecosystems characterized by frequent disturbance and abundant ecological opportunity (Whittaker, 1995; Whittaker and Fernández-Palacios, 2007; Whittaker et al., 2008). The combined effects of the dispersal and environmental filters during the colonization of an oceanic archipelago (Figure 2) results in an unusual abundance of unoccupied habitats and unexploited resources (Figure 3A), providing ecological opportunity for the establishment of hybrids generated during the diversification of successful colonist lineages. The amount of ecological opportunity in the form of unoccupied habitats depends, in part, on the size of the island and its distance from source populations, with larger and more distant islands providing more opportunity for *in situ* diversification – resulting in greater endemic richness (Whittaker and Fernández-Palacios, 2007; Whittaker et al., 2008). Endemic species richness, in turn, likely contributes to the overall frequency of hybridization observed on an island, given that secondary contact among members of young endemic clades is more likely to result in hybridization than secondary contact between species separated by greater divergence (Section 3, Figure 4).

Given the apparent importance of ecological segregation in maintaining species barriers on islands (Crawford and Archibald, 2017), frequent disturbance may regularly break down those barriers and facilitate secondary contact – regardless of the outcome of heterospecific mating. Specifically, frequent natural sources of disturbance on islands which may disrupt adaptive landscapes and facilitate secondary contact include storms such as hurricanes, wave action such as tsunamis, climate events, and volcanic activity. Examples of insular hybrids associated with such disturbed habitats include lava-colonizing silverswords (Caraway et al., 2001), *Coprosma* associated with climatic instability in New Zealand (Wichman et al., 2002)*,* and Galápagos finches (*Geospiza*) following a severe drought on Daphne island (Grant and Grant, 2016). Human induced disturbance on islands such as agriculture, deforestation, and urban development can also promote secondary contact (Caujapé-Castells et al., 2010; Vilà et al., 2000; Whittaker, 1995). For example, hybrids between three endemic species of *Pericallis* were associated with

the construction of roads in the Canaries (van Hengstum et al., 2012), hybrids of *Kunzea* were associated with disturbance by logging and fire in New Zealand (de Lange and Norton, 2004), hybrids of *Argyranthemum* were found in deforested environments in the Canaries (Brochmann et al., 2000), and hybrids of *Gunnera* were associated with human disturbed areas in the Juan Fernandez islands (Pacheco et al., 1991). These examples reinforce the general argument that ecological segregation plays an important role in maintaining species barriers on islands in the absence of intrinsic postzygotic barriers, but they also demonstrate that those barriers are not temporally stable, leading to occasional bouts of hybridization when disturbed.

(b) Long-distance dispersal

As a consequence of the great distances that often separate continents and islands, insular species characteristically possess long-distance dispersal capacities (Baker, 1955; Cain et al., 2000; Howe and Smallwood, 1982; Weigelt et al., 2015). For species that are not sympatric, a large dispersal shadow may facilitate secondary contact and thus hybridization (Figure 3B). If the species are interfertile, then once secondary contact is made, the size of the resultant hybrid zone will be governed by the relative magnitudes of dispersal and selection against hybrids (Barton and Hewitt, 1985; Endler, 1977). All other things being equal, insular species with long-distance dispersal capacities would be expected to form relatively larger hybrid zones upon secondary contact. Additionally, long-distance dispersal may facilitate the colonization of open or disturbed habitats, aiding in the establishment of hybrid lineages that do not require ongoing heterospecific mating for population maintenance.

Long-distance dispersal by wind or water can also overcome the isolation among islands in an archipelago. Even when relatively rare, such events can have a profound impact if migrants survive and reproduce where related species have already become established. A remarkable recent example of this in animals is the long-distance dispersal of a single finch over 100km between islands in the Galápagos that led to hybridization with local residents and the incipient formation of a new hybrid lineage reproductively isolated from parental species via mate call preference (Lamichhaney et al., 2017).

These considerations suggest that premating barriers in the form of geographic isolation may be counterintuitively weak for islands – at least occasionally. This prediction is tempered somewhat by the occurrence of insular taxa that have lost their long-distance dispersal capacities.

Loss of dispersal has undoubtedly occurred in many plant and animal groups (Bertrand et al., 2014; Carlquist, 1974), but the generality of this phenomenon is a matter of some debate (Burns, 2017; García-Verdugo et al., 2017). For these lineages, the predicted effect of dispersal may be reversed, with short-distance dispersal resulting in strong geographic isolation between species, or even populations of the same species. For example, a reduced propensity to disperse appears to be associated with strong population structure in the passerine bird *Zosterops borbonicus* endemic to Reunion Island (Bertrand et al., 2014).

(c) Compromised assortative mating

After long-distance dispersal events, secondary contact often involves a locally rare migrant species and a more abundant resident species. In such situations, assortative mating can break down as a result of the encounter rate between migrants being much lower than the encounter rate between the migrant and more abundant resident species – i.e. Hubb's Desperation Hypothesis (Hubbs, 1955; see also Kaneshiro, 1980 for a discussion of less complex mate recognition systems in colonizing populations). As a result, hybridization is expected to occur with greater frequency in situations where species proportions are numerically skewed (Rieseberg, 1997), or when it involves newly founded colonist populations (Kaneshiro, 1980). Indeed, many examples of hybridization are associated with situations of colonization and range expansion (Abbott et al., 2003; Arnold, 1997; Barton, 2001; Guo, 2014; Lamichhaney et al., 2017; Thompson, 1991) which often involve skewed species abundances, although it should be noted that in many cases it is unclear whether or not hybridization was a cause or consequence of colonization (see below).

Colonization is, of course, a frequent phenomenon on islands, given the availability of open/disturbed habitats and the long-distance dispersal capacities of many insular species. This may include both primary colonization events by continental taxa and secondary colonization events by already established insular lineages. An example of the former is secondary contact between insular and continental sister species of cotton (*Gossypium*) in the Galápagos which led to introgressive hybridization (Wendel and Percy, 1990), whereas the latter is exemplified by the aforementioned secondary contact event between finch species in the Galápagos following migration between islands (Lamichhaney et al., 2017). Compromised assortative mating during such colonization events likely contributes to the apparent frequency of hybridization on islands.

For insular floras, the breakdown of assortative mating may be further exacerbated by the greater dependence on generalist pollinators (Figure 3C). Being limited to successful dispersers, insular ecosystems are characterized by low pollinator richness (Levin et al., 1996; Olesen et al., 2002; Rodríguez-Rodríguez et al., 2013). Of the pollinators that have colonized islands, small insects represent a disproportionately large number due to their long-distance dispersal capacities (Barrett et al., 1996). These species – such as flies, moths, bees, and wasps – tend to be promiscuous pollinators, visiting many plant taxa (Barrett et al., 1996). Consequently, generalized pollination networks are common on oceanic islands, often including super-generalist species that indiscriminately pollinate a wide range of plant species (Carlquist, 1974; Kaiser-Bunbury et al., 2010; Olesen et al., 2002; Rodríguez-Rodríguez et al., 2013).

Super-generalists include a diverse range of taxa such as butterflies (*Leptotes parrhasioides,* Galápagos (Traveset et al., 2013)), beetles (*Mausoleopsis aldabrensis*, Aldabra (Woodell, 1979)), geckos (*Phelsuma ornate,* Mauritius (Olesen et al., 2002)), and most commonly bees (*Xylocopa darwini*, Galápagos (Traveset et al., 2013); *Halictus sp.,* the Azores (Olesen et al., 2002); *Anthophora allouardii* and *Bombus canariensis,* the Canaries (Olesen et al., 2002). For example, the Galápagos carpenter bee *Xylocopa darwini* has been documented to visit an astonishing 68% of plant species (84 of 123 plant species included in a review of Galápagos pollination literature) (Chamorro et al., 2012; Traveset et al., 2013) including many invasive taxa. Indiscriminate pollination directly promotes hybridization by increasing the rate of interspecific pollen exchange. It may also facilitate the establishment of hybrid offspring, since genotypes that express novel or intermediate floral characteristics are still likely to be visited by generalist pollinators. Pollinator-mediated assortative mating is one of the principle premating reproductive isolation barriers in plants (Kennedy et al., 2006; Schemske and Bradshaw, 1999; Temeles et al., 2016), and its apparent scarcity on islands is likely a key promoter of hybridization for insular floras.

An exception to this prediction can be seen in taxa that exclusively self-pollinate. Insular floras are enriched for self-compatibility – a phenomenon commonly known as Baker's Law (Grossenbacher et al., 2017). However, self-compatibility does not preclude some outbreeding (or outcrossing, in plants), and insular floras include a range of degrees of self-fertilization (Grossenbacher et al., 2017). Therefore, generalist pollination networks on islands will promote hybridization for all but exclusively self-pollinated species.

5. Consequences of heterospecific mating on islands

Much has already been written about the various outcomes of secondary contact, and especially of hybridization. For example, see Pfennig et al. (2016) for a review of hybridization and range expansion, Abbott et al. (2013) for hybridization and speciation, Seehausen (2004) for hybridization and adaptive radiation, and Todesco et al. (2016) for hybridization and extinction. The point we wish to emphasize here is that the most likely evolutionary trajectories will differ for cases of secondary contact between island natives versus contact between native and introduced species, and that this is relevant to contemporary conservation efforts.
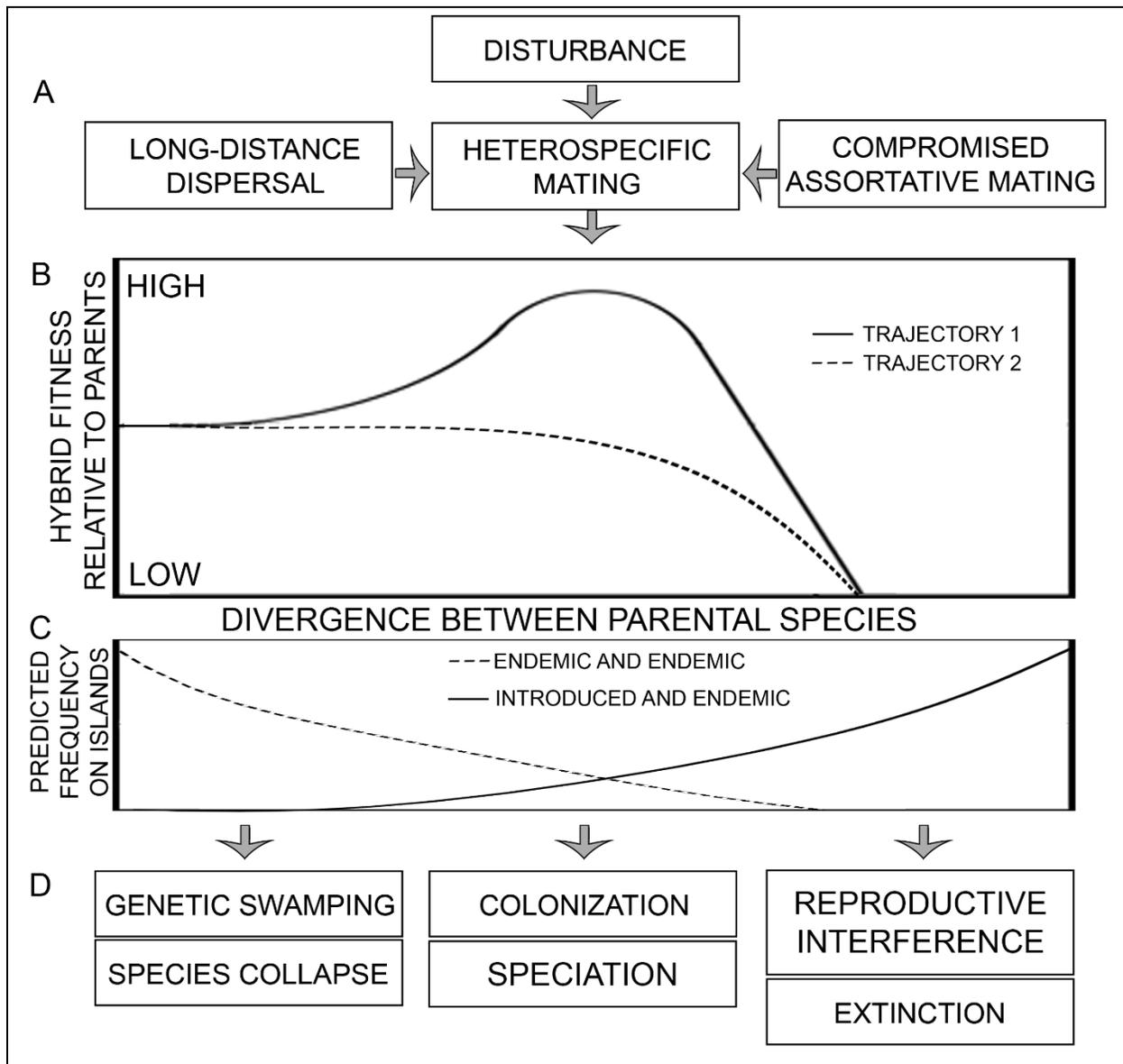
Figure 4. Generalized framework for understanding the causes and consequences of heterospecific mating on islands.

A) Disturbance, compromised assortative mating, and long-distance dispersal capacities promote secondary contact and heterospecific mating regardless of hybrid fitness and parental types (Section 4). B) If the species are interfertile, F1 hybrid fitness is predicted to depend in part on divergence between parental species, with fitness at first being approximately neutral to slightly lower for hybrids produced between very recently diverged species. With increasing divergence, hybrid fitness may then increase until eventually being outweighed by the accumulation of intrinsic incompatibilities (modified from (Ellstrand and Schierenbeck, 2000); trajectory 1), or steadily decrease due to both intrinsic and extrinsic barriers between species of increasing divergence (trajectory 2). C) Cases of secondary contact between insular endemics (dashed line) will be enriched for short divergence times, whereas cases of secondary contact between endemic and introduced species (solid line) will be enriched for relatively greater divergence times (Section 3). D) This leads to the prediction that outcomes of secondary contact between island endemics are enriched for genetic swamping and species collapse while outcomes of hybridization between native and introduced species are enriched for reproductive interference and extinction.

(a) Heterospecific mating between native species

Given that weak intrinsic barriers typically separate species within endemic clades on islands (Section 3), outcomes of mating that involve gene flow and the establishment of hybrid lineages are more likely (Figure 4). Indeed, multiple hybrid swarms have been described in association with disturbed habitats on islands (Morgan-Richards et al., 2009; Morley, 1971; Ruhsam et al., 2011), and late generation hybrids may even eventually replace one or both of the parental species through genetic swamping (Todesco et al., 2016). For example, *Argyranthemum coronopifolium* of Tenerife (Canary Islands) underwent rapid genetic swamping after secondary contact was initiated with widespread *A. frutescens* by the construction of roadways (Brochmann, 1984; Levin et al., 1996). Similarly, in Galápagos finches (*Geospiza*), widespread introgressive hybridization following a natural environmental disturbance contributed to the breakdown of reproductive barriers between species on Daphne island (Grant and Grant, 2016). These examples illustrate both the importance of extrinsic postzygotic barriers in maintaining

species boundaries on islands in the absence of other postmating barriers (Crawford and Archibald, 2017), and how frequent disturbance on islands may disrupt such barriers, thereby promoting hybridization. Such introgressive hybridization and species collapse is not inherently maladaptive – in some cases it may be favored by natural selection (Grant and Grant, 2016). For example, in Galápagos tree finches (*Camarhynchus*) on Floreana island, the persistence of hybrids and eventual species collapse may have involved hybrids being resistant to a novel parasite (Kleindorfer et al., 2014) – demonstrating that within a novel environment, hybrids can have a fitness advantage over parental individuals.

There are a number of ways in which interspecific gene flow can overcome mutational limits on adaptation and thereby facilitate establishment within a novel environment, including by producing an overall increase in standing genetic variation (Ellstrand and Schierenbeck, 2000; Grant and Grant, 2008; Lewontin and Birch, 1966; Pfennig et al., 2016), by producing novel or extreme phenotypes (transgressive segregation) (Reatini and Vision, 2020; Rieseberg et al., 1999, 2007), and by the transfer of adaptive alleles between species (adaptive introgression) (Arnold, 1997; Pfennig et al., 2016; Reatini and Vision, 2020b; Rieseberg et al., 2007; Seehausen, 2004). The likelihood of these beneficial effects of gene flow increase with genetic distance (Ellstrand and Schierenbeck, 2000; Stelkens and Seehausen, 2009). Generally, we would expect the fitness of early-generation hybrid offspring to increase with increasing genetic distance between parental species until a point where intrinsic incompatibilities begin to outweigh the beneficial effects, as illustrated in Figure 4B. Yet intrinsic barriers between endemic taxa are weak on islands (Section 3). Thus, hybridization among more divergent endemic taxa may be more likely to experience the beneficial effects of interspecific gene flow without suffering from strong intrinsic barriers (Figure 4B). The resulting hybrids may be capable of colonizing novel environments, particularly given the abundant ecological opportunity on islands (Section 4a)

After the successful establishment of a hybrid population, homoploid hybrid speciation can occur if extrinsic isolation from its parental species is strong enough (Yakimowski and Rieseberg, 2014). Alternatively, hybridization can result in the generation of allopolyploid hybrids – polyploid offspring with a copy of both parental genomes. In such cases, novel phenotypes and resulting range expansion can be coupled with nearly instantaneous speciation, given that polyploid offspring are often reproductively isolated from diploid parental species

(Abbott et al., 2013; Thompson, 1991) although see (Ramsey and Schemske, 1998). Cases of allopolyploid hybrid speciation appear to be more common in plants, while homoploid speciation seems to be more common in animals (Abbott et al., 2013). On islands, proposed cases of allopolyploid hybrid speciation include the entire silversword alliance in Hawaii (Barrier et al., 1999), members of *Lepidium* (Dierschke et al., 2009) and *Pachycladon* (Mandáková et al., 2010) in New Zealand and Tasmania, and *Dryopteris* in the Azores (Gibby, 1985). Proposed cases of homoploid hybrid speciation include members of *Geospiza* in the Galápagos (Lamichhaney et al., 2017), *Argyranthemum* in the Canaries (Brochmann et al., 2000), *Scaevola* in Hawaii (Howarth and Baum, 2005), *Artibeus* in the Caribbean (Larsen et al., 2010), and *Acanthoxyla* in New Zealand (Morgan-Richards and Trewick, 2005). The latter example offers a remarkable display of hybrid speciation whereby eight species of parthenogenic stick insects were derived from multiple hybridization events between two or three sexual ancestors.

When sufficient ecological opportunity is available, hybridization may also play a role in facilitating adaptive radiation (Seehausen, 2013). Since ecological opportunity is a hallmark of islands (Section 4.1.), it is perhaps unsurprising that many insular radiations are proposed to have involved hybridization. Among these are *Aeonium* (Jorgensen and Olesen, 2001) and *Argyranthemum* (Francisco-Ortega et. al., 1997) in the Canaries, *Cyprinodon* in the Caribbean (Richards and Martin, 2017), *Laupala* (Shaw, 2002), *Cyrtandra* (Smith et al., 1996), and the silversword alliance (Barrier et al., 1999) of Hawaii, and *Pachycladon* in New Zealand and Tasmania (Mandáková et al., 2010). However, as Seehausen (2004) has cautioned, demonstrating that hybridization preceded an adaptive radiation is not sufficient to conclude that hybridization was a cause of the adaptive radiation. Disentangling the factors by which hybridization can lead to colonization, allopolyploid/homoploid hybrid speciation, reinforcement, or adaptive radiation requires detailed knowledge of the system in question (Seehausen, 2013). The simplified ecological contexts of islands and the diversity of systems for which hybridization is known to occur, often within the same radiation, make insular species attractive systems in which to study these processes (Crawford and Archibald, 2017).

(b) Heterospecific mating between native and introduced species
Islands have been subject to an alarming number of species introductions as a result of human activities, with the Pacific islands showing the fastest increase in species numbers with

respect to their land areas of all ecosystems included in a recent study (van Kleunen et al., 2015). A striking result of these introductions is the observed doubling of net plant species richness across many oceanic archipelagos world-wide (Sax and Gaines, 2008). In both Hawaii and the Galápagos for example, roughly a third of all native vascular plant genera now also contain at least one introduced species (33% and 30% respectively) (Jaramillo et al., 2018, USDA, NRCS, 2019). Thus, such an influx of species on islands provides substantial opportunity for secondary contact and subsequent mating between formerly isolated native and introduced congeners.

Mating between native and introduced species can create a number of unique problems for the conservation of island biodiversity. Hybridization with introduced species can result in a net decrease of native biodiversity when continuous hybridization and backcrossing of hybrids with parental species results in the replacement of a parental species with hybrids (genetic swamping), or when the production of low fitness hybrids results in the extinction of a parental species due to wasted reproductive effort (i.e. resulting from reproductive interference) (Todesco et al., 2016). However, even when hybrids are not produced, interspecific mating can jeopardize coexistence. Reproductive interference generally refers to any negative sexual interaction that leads to a reduction of fitness for at least one parental population (Kyogoku, 2020), and can occur in a variety of ways that don't involve fertilization including stigma clogging or pollen competition in plants or injury during copulation for animals (Gröning and Hochkirch, 2008; Kyogoku, 2020; Kyogoku and Sota, 2017). The term demographic swamping has been used in the literature to describe reproductive interference when low fitness hybrids are produced (Todesco et al., 2016), but it is important to note that all types of reproductive interference result in wasted reproductive effort and can ultimately lead to demographic decline if prezygotic barriers don't evolve to prevent maladaptive mating (i.e. reinforcement) (Kyogoku, 2020) – which can indeed occur on rapid timescales (Pfennig, 2003).

Based on our framework above, we would predict that genetic swamping is more likely among endemic clades due to recent divergence between parental species (Section 5a, Figure 4), while reproductive interference is more likely when mating occurs between endemic and introduced species (Figure 4). This is in part because the upper limit on divergence imposed by islands for endemic clades represents a lower limit on divergence times between endemic and introduced species, given that they must have evolved in allopatry since at least the age of the

endemic lineage. Thus, postzygotic barriers are more likely to be observed when mating occurs between endemic and introduced species than for pairs of endemic species.

The impacts of reproductive interference are expected to be more pronounced between numerically skewed species (Kishi et al., 2009; Kyogoku and Sota, 2017), such as in the common scenario of a widespread invasive species and a localized, endemic congener. For example, if a native plant is surrounded by an invasive congener, there is a high probability of pollen transfer from an invasive individual relative to native plants in populations with lower invasive abundance. If there are fitness consequences of such interspecific pollen transfer, extirpation of the less abundant species by reproductive interference is likely.

Reproductive inference might be common yet difficult to detect, due to hybrid individuals being scarce or entirely absent. Indeed, the detection of reproductive interference often requires intensive experiments to test the diversity of ways sexual interactions can lead to reduced parental fitness (Gröning and Hochkirch, 2008; Kyogoku, 2020). Moreover, observing the contribution of reproductive interference to ongoing local exclusion is empirically difficult due to the speed with which it is expected to be resolved (Kyogoku, 2020). As a result, the effects of reproductive interference may be attributed to other factors such as competition or be overlooked entirely. Although a number of studies have investigated whether there are undesirable outcomes of hybridization between native and introduced species on islands, they have often done so by examining the extent of gene flow (González-Pérez and Sosa, 2009; Levin et al., 1996; López-Caamal et al., 2014; Milián-García et al., 2015). Thus, they may fail to detect one of the most likely threats of such hybridization – wasted reproductive effort due to reproductive interference. The alarming number of species introductions on islands (Sax and Gaines, 2008) unfortunately means that there is an abundance and diversity of systems in which to explore the consequences of reproductive interference, and to do so within a context that is highly relevant for conservation efforts. Thus, reproductive interference likely represents an underappreciated conservation threat to native biodiversity on islands and is ripe for further research effort.

In the rare cases where hybrids between native and introduced species survive to reproduction and are capable of backcrossing with parental species, hybrid invasion poses a different kind of conservation threat. Hybridization can facilitate the initial colonization of introduced species by alleviating Allee effects common in founding populations, *i.e.* overcoming

the minimum density threshold for population viability due to mate availability (Hubbs, 1955; Mesgaran et al., 2016; Taylor and Hastings, 2005). Subsequent gene flow may then contribute to local adaptation in established introduced populations (Gibson et al., 2021) – which may favor their persistence – or directly contribute to range expansion (invasion) of introduced species by the same means described for native species pairs (Section 5a). Both hybridization and invasion are commonly discussed independently as important threats to native island biodiversity, but given the relationship between hybridization and colonization, it is likely that these two threats are related.

6. Conclusions

We conclude that there are two faces of secondary contact on islands given the dramatic differences in expected outcomes of secondary contact for native species pairs versus native and introduced species pairs. This rests on a few assertions. First, that for all taxa secondary contact occurs frequently on islands as a result of the long-distance dispersal capacities of insular species and frequent disturbance within insular ecosystems, and that compromised assortative mating frequently results in heterospecific mating within these zones of secondary contact. Second, that when members of endemic clades come into secondary contact on islands, heterospecific mating will frequently result in the establishment and persistence of hybrids due to weak intrinsic postzygotic barriers and abundant ecological opportunity on islands providing suitable habitats. By contrast, when native and introduced species come into secondary contact on islands, local exclusion via reproductive interference will be common due to the relatively greater degree of intrinsic postzygotic isolation between such species pairs. While the first face of secondary contact, that between endemic species, likely explains the apparent frequency of hybridization on islands, the second face, that between native and introduced species, represents a potentially significant, cryptic, and thus underappreciated threat to native island biodiversity.

Data availability: All information is included within the manuscript.

References

Abbott, R., Albach, D., Ansell, S., Arntzen, J.W., Baird, S.J.E., Bierne, N., Boughman, J., Brelsford, A., Buerkle, C.A., Buggs, R., et al. (2013). Hybridization and speciation. J. Evol. Biol. *26*, 229–246.

Abbott, R.J., James, J.K., Milne, R.I., and Gillies, A.C.M. (2003). Plant introductions, hybridization and gene flow. Philos. Trans. R. Soc. B Biol. Sci. *358*, 1123–1132.

Anderson, E. (1948). Hybridization of the Habitat. Evolution *2*, 1–9.

Arnold, M.L. (1997). Natural Hybridization and Evolution. (Cary: Oxford University Press).

Baker, H.G. (1955). Self-Compatibility and Establishment After "Long-Distance" Dispersal. Evolution *9*, 347.

Baldwin, B.G., and Sanderson, M.J. (1998). Age and rate of diversification of the Hawaiian silversword alliance (Compositae). Proc. Natl. Acad. Sci. *95*, 9402–9406.

Barrett, S.C.H., Emerson, B., and Mallet, J. (1996). The Reproductive Biology and Genetics of Island Plants [and Discussion]. Philos. Trans. Biol. Sci. *351*, 725–733.

Barrier, M., Baldwin, B.G., Robichaux, R.H., and Purugganan, M.D. (1999). Interspecific hybrid ancestry of a plant adaptive radiation: allopolyploidy of the Hawaiian silversword alliance (Asteraceae) inferred from floral homeotic gene duplications. Mol. Biol. Evol. *16*, 1105–1113.

Barton, N.H. (2001). The role of hybridization in evolution. Mol. Ecol. *10*, 551–568.

Barton, N.H., and Hewitt, G.M. (1985). Analysis of Hybrid Zones. Annu. Rev. Ecol. Syst. *16*, 113–148.

Bertrand, J. a. M., Bourgeois, Y.X.C., Delahaie, B., Duval, T., García-Jiménez, R., Cornuault, J., Heeb, P., Milá, B., Pujol, B., and Thébaud, C. (2014). Extremely reduced dispersal and gene flow in an island bird. Heredity *112*, 190–196.

Borgen, L., Leitch, I., and Santos-Guerra, A. (2003). Genome organization in diploid hybrid species of Argyranthemum (Asteraceae) in the Canary Islands. Bot. J. Linn. Soc. *141*, 491–501.

Brill, E., Kang, L., Michalak, K., Michalak, P., and Price, D.K. (2016). Hybrid sterility and evolution in Hawaiian Drosophila: differential gene and allele-specific expression analysis of backcross males. Heredity *117*, 100–108.

Brochmann, C. (1984). Hybridization and distribution of Argyranthemum coronopifolium (Asteraceae – Anthemideae) in the Canary Islands. Nord. J. Bot. *4*, 729–736.

Brochmann, C., Borgen, L., and Stabbetorp, O.E. (2000). Multiple diploid hybrid speciation of the Canary Island endemic Argyranthemum sundingii (Asteraceae). Plant Syst. Evol. *220*, 77–92.

Buckley, T.R., Attanayake, D., Park, D., Ravindran, S., Jewell, T.R., and Normark, B.B. (2008). Investigating hybridization in the parthenogenetic New Zealand stick insect Acanthoxyla (Phasmatodea) using single-copy nuclear loci. Mol. Phylogenet. Evol. *48*, 335–349.

Burns, K.C. (2017). Time to abandon the loss of dispersal ability hypothesis in island plants: A comment on García-Verdugo, Mairal, Monroy, Sajeva and Caujapé-Castells. J. Biogeogr. *45*, 1219–1222.

Cain, M.L., Milligan, B.G., and Strand, A.E. (2000). Long-distance seed dispersal in plant populations. Am. J. Bot. *87*, 1217–1227.

Campbell, D.R., and Waser, N.M. (2001). Genotype-by-environment interaction and the fitness of plant hybrids in the wild. Evolution *55*, 669–676.

Caraway, V., Carr, G.D., and Morden, C.W. (2001). Assessment of Hybridization and Introgression in Lava-Colonizing Hawaiian Dubautia (Asteraceae: Madiinae) Using RAPD Markers. Am. J. Bot. *88*, 1688.

Carlquist, S.J. (1974). Island biology (New York: Columbia University Press).

Carr, G.D., and Kyhos, D.W. (1986). Adaptive Radiation in the Hawaiian Silversword Alliance (compositae-Madiinae). Ii. Cytogenetics of Artificial and Natural Hybrids. Evolution *40*, 959–976.

Carr, G.D., Baldwin, B.G., and Kyhos, D.W. (1996). Cytogenetic implications of artificial hybrids between the hawaiian silversword alliance and North American tarweeds (Asteraceae: Heliantheae—Madiinae). Am. J. Bot. *83*, 653–660.

Carson, H.L., Kaneshiro, K.Y., and Val, F.C. (1989). Natural Hybridization Between the Sympatric Hawaiian Species Drosophila Silvestris and Drosophila Heteroneura. Evolution *43*, 190–203.

Carvajal-Endara, S., Hendry, A.P., Emery, N.C., and Davies, T.J. (2017). Habitat filtering not dispersal limitation shapes oceanic island floras: species assembly of the Galápagos archipelago. Ecol. Lett. *20*, 495–504.

Caujapé-Castells, J., Tye, A., Crawford, D.J., Santos-Guerra, A., Sakai, A., Beaver, K., Lobin, W., Vincent Florens, F.B., Moura, M., and Jardim, R. (2010). Conservation of oceanic island floras: Present and future global challenges. Perspect. Plant Ecol. Evol. Syst. *12*, 107–129.

Chamorro, S., Heleno, R., Olesen, J.M., McMullen, C.K., and Traveset, A. (2012). Pollination patterns and plant breeding systems in the Galápagos: a review. Ann. Bot. *110*, 1489–1501.

Crawford, D.J., and Archibald, J.K. (2017). Island floras as model systems for studies of plant speciation: Prospects and challenges. J. Syst. Evol. *55*, 1–15.

Crawford, D.J., Hauber, D.P., Silva, L.B., Sequeira, M.M. de, Moura, M., Santos-Guerra, A., Kelly, J.K., and Mort, M.E. (2016). Breeding Relationships in Macaronesian Tolpis (Asteraceae-Cichorieae): F1 Hybrid Pollen Fertility Within and Among Populations from the Azores, Canary Islands, and Madeira. Syst. Bot. *41*, 881–893.

Dalgaard, V. (1979). Biosystematics of the Macaronesian species of Scrophularia (Lund, Sweden; Stockholm, Sweden: Lund Botanical Society ; Swedish Natural Science Research Council).

Dierschke, T., Mandáková, T., Lysak, M.A., and Mummenhoff, K. (2009). A bicontinental origin of polyploid Australian/New Zealand Lepidium species (Brassicaceae)? Evidence from genomic in situ hybridization. Ann. Bot. *104*, 681–688.

Dowle, E.J., Morgan-Richards, M., and Trewick, S.A. (2014). Morphological differentiation despite gene flow in an endangered grasshopper. BMC Evol. Biol. *14*, 216.

Ellstrand, N.C., and Schierenbeck, K.A. (2000). Hybridization as a stimulus for the evolution of invasiveness in plants? Proc. Natl. Acad. Sci. *97*, 7043–7050.

Endler, J.A. (1977). Geographic Variation, Speciation, and Clines (Princeton University Press).

Fernández-Palacios, J.M., Nascimento, L. de, Otto, R., Delgado, J.D., García-del-Rey, E., Arévalo, J.R., and Whittaker, R.J. (2011). A reconstruction of Palaeo-Macaronesia, with particular reference to the long-term biogeography of the Atlantic island laurel forests. J. Biogeogr. *38*, 226–246.

Fitzpatrick, B.M. (2004). Rates of evolution of hybrid inviability in birds and mammals. Evol. Int. J. Org. Evol. *58*, 1865–1870.

Friar, E.A., Prince, L.M., Cruse-Sanders, J.M., McGlaughlin, M.E., Butterworth, C.A., and Baldwin, B.G. (2008). Hybrid Origin and Genomic Mosaicism of Dubautia scabra (Hawaiian Silversword Alliance; Asteraceae, Madiinae). Syst. Bot. *33*, 589–597.

García-Verdugo, C., Friar, E., and Santiago, L.S. (2013). Ecological Role of Hybridization in Adaptive Radiations: A Case Study in the Dubautia arborea–Dubautia ciliolata (Asteraceae) Complex. Int. J. Plant Sci. *174*, 749–759.

García-Verdugo, C., Mairal, M., Monroy, P., Sajeva, M., and Caujapé-Castells, J. (2017). The loss of dispersal on islands hypothesis revisited: Implementing phylogeography to investigate evolution of dispersal traits in Periploca (Apocynaceae). J. Biogeogr. *44*, 2595–2606.

Garrick, R.C., Benavides, E., Russello, M.A., Hyseni, C., Edwards, D.L., Gibbs, J.P., Tapia, W., Ciofi, C., and Caccone, A. (2014). Lineage fusion in Galápagos giant tortoises. Mol. Ecol. *23*, 5276–5290.

Gibby, M. (1985). Hybridization and speciation in the genus Dryopteris (Pteridophyta:Dryopteridaceae) on Pico Island in the Azores. Plant Syst. Evol. *149*, 241–252.

Gibson, M.J., Torres, M. de L., Brandvain, Y., and Moyle, L. (2021). Introgression shapes fruit color convergence in invasive Galápagos tomato. ELife *10*, e64165.

González-Pérez, M.A., and Sosa, P.A. (2009). Hybridization and Introgression Between the Endemic Phoenix canariensis and the Introduced P. dactylifera in the Canary Islands. Open For. Sci. J. *2*, 78–85.

Grabenstein, K.C., and Taylor, S.A. (2018). Breaking Barriers: Causes, Consequences, and Experimental Utility of Human-Mediated Hybridization. Trends Ecol. Evol. *33*, 198–212.

Grant, B.R., and Grant, P.R. (2008). Fission and fusion of Darwin's finches populations. Philos. Trans. R. Soc. B Biol. Sci. *363*, 2821–2829.

Grant, P.R., and Grant, B.R. (2016). Introgressive hybridization and natural selection in Darwin's finches. Biol. J. Linn. Soc. *117*, 812–822.

Gröning, J., and Hochkirch, A. (2008). Reproductive Interference Between Animal Species. Q. Rev. Biol. *83*, 257–282.

Grossenbacher, D.L., Brandvain, Y., Auld, J.R., Burd, M., Cheptou, P.-O., Conner, J.K., Grant, A.G., Hovick, S.M., Pannell, J.R., Pauw, A., et al. (2017). Self-compatibility is over-represented on islands. New Phytol. *215*, 469–478.

Guo, Q. (2014). Plant hybridization: the role of human disturbance and biological invasion. Divers. Distrib. *20*, 1345–1354.

van Hengstum, T., Lachmuth, S., Oostermeijer, J.G.B., den Nijs, H. (J.) C.M., Meirmans, P.G., and van Tienderen, P.H. (2012). Human-induced hybridization among congeneric endemic plants on Tenerife, Canary Islands. Plant Syst. Evol. *298*, 1119–1131.

Houliston, G.J., Heenan, P.B., and Smissen, R.D. (2008). Experimental crosses in Phormium confirm the lack of intrinsic barriers to interspecific hybridisation and the fertility of putative wild hybrids. N. Z. J. Bot. *46*, 393–399.

Howarth, D.G., and Baum, D.A. (2005). Genealogical Evidence of Homoploid Hybrid Speciation in an Adaptive Radiation of Scaevola (goodeniaceae) in the Hawaiian Islands. Evolution *59*, 948–961.

Howe, H.F., and Smallwood, J. (1982). Ecology of Seed Dispersal. Annu. Rev. Ecol. Syst. *13*, 201–228.

Hubbs, C.L. (1955). Hybridization between Fish Species in Nature. Syst. Zool. *4*, 1–20.

Jaramillo P, Guézou A, Mauchamp A, Tye A. 2018. CDF Checklist of Galápagos Flowering Plants - FCD Lista de especies de Plantas con flores de Galápagos. In: Bungartz F, Herrera H, Jaramillo P, Tirado N, Jiménez-Uzcátegui G, Ruiz D, Guézou A, Ziemmeck F, editors. Charles Darwin Foundation Galápagos Species Checklist - Lista de Especies de Galápagos de la Fundación Charles Darwin. Puerto Ayora, Galápagos: Charles Darwin Foundation / Fundación Charles Darwin.

Jorgensen, T.H., and Olesen, J.M. (2001). Adaptive radiation of island plants: evidence from Aeonium (Crassulaceae) of the Canary Islands. Perspect. Plant Ecol. Evol. Syst. *4*, 29–42.

Kaiser-Bunbury, C.N., Traveset, A., and Hansen, D.M. (2010). Conservation and restoration of plant–animal mutualisms on oceanic islands. Perspect. Plant Ecol. Evol. Syst. *12*, 131–143.

Kaneshiro, K.Y. (1980). Sexual Isolation, Speciation and the Direction of Evolution. Evolution *34*, 437–444.

Kaneshiro, K.Y., and Val, F.C. (1977). Natural Hybridization between a Sympatric Pair of Hawaiian Drosophila. Am. Nat. *111*, 897–902.

Kennedy, B.F., Sabara, H.A., Haydon, D., and Husband, B.C. (2006). Pollinator-mediated assortative mating in mixed ploidy populations of Chamerion angustifolium (Onagraceae). Oecologia *150*, 398–408.

Kishi, S., Nishida, T., and Tsubaki, Y. (2009). Reproductive interference determines persistence and exclusion in species interactions. J. Anim. Ecol. *78*, 1043–1049.

Kleindorfer, S., O'Connor, J.A., Dudaniec, R.Y., Myers, S.A., Robertson, J., and Sulloway, F.J. (2014). Species Collapse via Hybridization in Darwin's Tree Finches. Am. Nat. *183*, 325–341.

van Kleunen, M., Dawson, W., Essl, F., Pergl, J., Winter, M., Weber, E., Kreft, H., Weigelt, P., Kartesz, J., Nishino, M., et al. (2015). Global exchange and accumulation of non-native plants. Nature *525*, 100–103.

Kreft, H., Jetz, W., Mutke, J., Kier, G., and Barthlott, W. (2008). Global diversity of island floras from a macroecological perspective. Ecol. Lett. *11*, 116–127.

Kyogoku, D. (2020). When does reproductive interference occur? Predictions and data. Popul. Ecol. *62*, 196–206.

Kyogoku, D., and Sota, T. (2017). A generalized population dynamics model for reproductive interference with absolute density dependence. Sci. Rep. *7*, 1996.

Lamichhaney, S., Han, F., Webster, M.T., Andersson, L., Grant, B.R., and Grant, P.R. (2017). Rapid hybrid speciation in Darwin's finches. Science *359*, 224–228.

de Lange, P.J., and Norton, D.A. (2004). The ecology and conservation of Kunzea sinclairii (Myrtaceae), a naturally rare plant of rhyolitic rock outcrops. Biol. Conserv. *117*, 49–59.

Larsen, P.A., Marchán-Rivadeneira, M.R., and Baker, R.J. (2010). Natural hybridization generates mammalian lineage with species characteristics. Proc. Natl. Acad. Sci. *107*, 11447–11452.

Levin, D.A. (2012). The long wait for hybrid sterility in flowering plants. New Phytol. *196*, 666–670.

Levin, D.A., Francisco-Ortega, J., and Jansen, R.K. (1996). Hybridization and the Extinction of Rare Plant Species. Conserv. Biol. *10*, 10–16.

Lewontin, R.C., and Birch, L.C. (1966). Hybridization as a Source of Variation for Adaptation to New Environments. Evolution *20*, 315–336.

Lindhardt, M.S., Philipp, M., Tye, A., and Nielsen, L.R. (2009). Molecular, Morphological, and Experimental Evidence for Hybridization between Threatened Species of the Galapagos Endemic Genus Scalesia (Asteraceae). Int. J. Plant Sci. *170*, 1019–1030.

López-Caamal, A., Cano-Santana, Z., Jiménez-Ramírez, J., Ramírez-Rodríguez, R., and Tovar-Sánchez, E. (2014). Is the insular endemic Psidium socorrense (Myrtaceae) at risk of extinction through hybridization? Plant Syst. Evol. *300*, 1959–1972.

Losos, J. (2009). Lizards in an Evolutionary Tree: Ecology and Adaptive Radiation of Anoles (Berkeley: University of California Press).

MacArthur, R.H., and Wilson, E.O. (1963). An Equilibrium Theory of Insular Zoogeography. Evolution *17*, 373–387.

MacLeod, A., Rodríguez, A., Vences, M., Orozco-terWengel, P., García, C., Trillmich, F., Gentile, G., Caccone, A., Quezada, G., and Steinfartz, S. (2015). Hybridization masks speciation in the evolutionary history of the Galápagos marine iguana. Proc R Soc B *282*, 20150425.

Mallet, J. (2005). Hybridization as an invasion of the genome. Trends Ecol. Evol. *20*, 229–237.

Mandáková, T., Heenan, P.B., and Lysak, M.A. (2010). Island species radiation and karyotypic stasis in Pachycladon allopolyploids. BMC Evol. Biol. *10*, 367.

Marques, D.A., Meier, J.I., and Seehausen, O. (2019). A Combinatorial View on Speciation and Adaptive Radiation. Trends Ecol. Evol. *34*, 531–544.

Mavárez, J., Salazar, C.A., Bermingham, E., Salcedo, C., Jiggins, C.D., and Linares, M. (2006). Speciation by hybridization in *Heliconius* butterflies. Nature *441*, 868–871.

Mayer, S.S. (1991). Artificial Hybridization in Hawaiian Wikstroemia (thymelaeaceae). Am. J. Bot. *78*, 122–130.

Mensch, J.A., and Gillett, G.W. (1972). The Experimental Verification of Natural Hybridization Between Two Taxa of Hawaiian Bidens (Asteraceae). Brittonia *24*, 57–70.

Mesgaran, M.B., Lewis, M.A., Ades, P.K., Donohue, K., Ohadi, S., Li, C., and Cousens, R.D. (2016). Hybridization can facilitate species invasions, even without enhancing local adaptation. Proc. Natl. Acad. Sci. *113*, 10210–10214.

Milián-García, Y., Ramos-Targarona, R., Pérez-Fleitas, E., Sosa-Rodríguez, G., Guerra-Manchena, L., Alonso-Tabet, M., Espinosa-López, G., and Russello, M.A. (2015). Genetic evidence of hybridization between the critically endangered Cuban crocodile and the American

crocodile: implications for population history and in situ/ex situ conservation. Heredity *114*, 272–280.

Milinkovitch, M.C., Monteyne, D., Russello, M., Gibbs, J.P., Snell, H.L., Tapia, W., Marquez, C., Caccone, A., and Powell, J.R. (2007). Giant Galápagos tortoises; molecular genetic analyses identify a trans-island hybrid in a repatriation program of an endangered taxon. BMC Ecol. *7*, 2.

Morgan-Richards, M., and Trewick, S.A. (2005). Hybrid origin of a parthenogenetic genus? Mol. Ecol. *14*, 2133–2142.

Morgan-Richards, M., Smissen, R.D., Shepherd, L.D., Wallis, G.P., Hayward, J.J., Chan, C., Chambers, G.K., and Chapman, H.M. (2009). A review of genetic analyses of hybridisation in New Zealand. J. R. Soc. N. Z. *39*, 15–34.

Morley, B.D. (1971). A hybrid swarm between two hummingbird-pollinated species of Columnea (Gesneriaceae) in Jamaica. Bot. J. Linn. Soc. *64*, 81–96.

Motley, T.J., and Carr, G.D. (1998). Artificial hybridization in the Hawaiian endemic genus Labordia (Loganiaceae). Am. J. Bot. *85*, 654–660.

Neall, V.E., and Trewick, S.A. (2008). The age and origin of the Pacific islands: a geological overview. Philos. Trans. R. Soc. B Biol. Sci. *363*, 3293–3308.

Nielsen, L.R., Cowan, R.S., Siegismund, H.R., Adsersen, H., Philipp, M., and Fay, M.F. (2003). Morphometric, AFLP and plastid microsatellite variation in populations of Scalesia divisa and S. incisa (Asteraceae) from the Galápagos Islands. Bot. J. Linn. Soc. *143*, 243–254.

Olesen, J.M., Eskildsen, L.I., and Venkatasamy, S. (2002). Invasion of pollination networks on oceanic islands: importance of invader complexes and endemic super generalists. Divers. Htmlent Glyphamp Asciiamp Distrib. *8*, 181–192.

Pacheco, P., Stuessy, T.F., and Crawford, D.J. (1991). Natural Interspecific Hybridization in Gunnera (Gunneraceae) of the Juan Fernandez Islands, Chile. *45*, 389–399.

Parham, J.F., Papenfuss, T.J., Dijk, P.P. van, Wilson, B.S., Marte, C., Schettino, L.R., and Brian Simison, W. (2013). Genetic introgression and hybridization in Antillean freshwater turtles (Trachemys) revealed by coalescent analyses of mitochondrial and cloned nuclear markers. Mol. Phylogenet. Evol. *67*, 176–187.

Pfennig, K.S. (2003). A Test of Alternative Hypotheses for the Evolution of Reproductive Isolation Between Spadefoot Toads: Support for the Reinforcement Hypothesis. Evolution *57*, 2842–2851.

Pfennig, K.S., Kelly, A.L., and Pierce, A.A. (2016). Hybridization as a facilitator of species range expansion. Proc. R. Soc. B Biol. Sci. *283*, 20161329.

Price, T.D., and Bouvier, M.M. (2002). The evolution of F1 postzygotic incompatibilities in birds. Evol. Int. J. Org. Evol. *56*, 2083–2089.

Puppo, P., Curto, M., and Meimberg, H. (2016). Genetic structure of Micromeria (Lamiaceae) in Tenerife, the imprint of geological history and hybridization on within-island diversification. Ecol. Evol. *6*, 3443–3460.

Ramsey, J., and Schemske, D.W. (1998). Pathways, mechanisms, and rates of polyploid formation in flowering plants. Annu. Rev. Ecol. Syst. *29*, 467–501.

Rassmann K., Trillmich F., and Tautz D. (2009). Hybridization between the Galápagos land and marine iguana (Canolophus subcristatus and Amblyrhynchus cristatus) on Plaza Sur. J. Zool. *242*, 729–739.

Reatini, B., and Vision, T.J. (2020). Genetic architecture influences when and how hybridization contributes to colonization. Evolution *74*, 1590–1602.

Richards, E.J., and Martin, C.H. (2017). Adaptive introgression from distant Caribbean islands contributed to the diversification of a microendemic adaptive radiation of trophic specialist pupfishes. PLOS Genet. *13*, e1006919.

Rieseberg, L.H. (1997). Hybrid Origins of Plant Species. Annu. Rev. Ecol. Syst. *28*, 359–389.

Rieseberg, L.H., Whitton, J., and Gardner, K. (1999). Hybrid Zones and the Genetic Architecture of a Barrier to Gene Flow Between Two Sunflower Species. Genetics *152*, 713–727.

Rieseberg, L.H., Kim, S.-C., Randell, R.A., Whitney, K.D., Gross, B.L., Lexer, C., and Clay, K. (2007). Hybridization and the colonization of novel habitats by annual sunflowers. Genetica *129*, 149–165.

Rodríguez-Rodríguez, M.C., Jordano, P., and Valido, A. (2013). Quantity and quality components of effectiveness in insular pollinator assemblages. Oecologia *173*, 179–190.

Ruhsam, M., Hollingsworth, P.M., and Ennos, R.A. (2011). Early evolution in a hybrid swarm between outcrossing and selfing lineages in Geum. Heredity *107*, 246–255.

Russell, J.C., and Kueffer, C. (2019). Island Biodiversity in the Anthropocene. Annu. Rev. Environ. Resour. *44*, 31–60.

Sax, D.F., and Gaines, S.D. (2008). Species invasions and extinction: The future of native biodiversity on islands. Proc. Natl. Acad. Sci. *105*, 11490–11497.

Schemske, D.W., and Bradshaw, H.D. (1999). Pollinator preference and the evolution of floral traits in monkeyflowers (Mimulus). Proc. Natl. Acad. Sci. *96*, 11910–11915.

Seehausen, O. (2004). Hybridization and adaptive radiation. Trends Ecol. Evol. *19*, 198–207.

Seehausen, O. (2013). Conditions when hybridization might predispose populations for adaptive radiation. J. Evol. Biol. *26*, 279–281.

Servedio, M.R., and Noor, M.A.F. (2003). The Role of Reinforcement in Speciation: Theory and Data. Annu. Rev. Ecol. Evol. Syst. *34*, 339–364.

Shaw, K.L. (2002). Conflict between nuclear and mitochondrial DNA phylogenies of a recent species radiation: What mtDNA reveals and conceals about modes of speciation in Hawaiian crickets. Proc. Natl. Acad. Sci. *99*, 16122–16127.

Smissen, R.D., and Heenan, P.B. (2007). DNA fingerprinting supports hybridisation as a factor explaining complex natural variation in Phormium (Hemerocallidaceae). N. Z. J. Bot. *45*, 419–432.

Smith, J.F., Burke, C.C., and Wagner, W.L. (1996). Interspecific hybridization in natural populations of Cyrtandra (Gesneriaceae) on the Hawaiian Islands: Evidence from RAPD markers. Plant Syst. Evol. *200*, 61–77.

Stelkens, R., and Seehausen, O. (2009). Genetic Distance Between Species Predicts Novel Trait Expression in Their Hybrids. Evolution *63*, 884–897.

Taylor, C.M., and Hastings, A. (2005). Allee effects in biological invasions. Ecol. Lett. *8*, 895–908.

Temeles, E.J., Newman, J.T., Newman, J.H., Cho, S.Y., Mazzotta, A.R., and Kress, W.J. (2016). Pollinator Competition as a Driver of Floral Divergence: An Experimental Test. PLOS ONE *11*, e0146431.

Thompson, J.D. (1991). The Biology of an Invasive Plant: What makes Spartina anglica so successful? BioScience *41*, 393–401.

Todesco, M., Pascual, M.A., Owens, G.L., Ostevik, K.L., Moyers, B.T., Hübner, S., Heredia, S.M., Hahn, M.A., Caseys, C., Bock, D.G., et al. (2016). Hybridization and extinction. Evol. Appl. *9*, 892–908.

Traveset, A., Heleno, R., Chamorro, S., Vargas, P., McMullen, C.K., Castro-Urgal, R., Nogales, M., Herrera, H.W., and Olesen, J.M. (2013). Invaders of pollination networks in the Galápagos Islands: emergence of novel communities. Proc. R. Soc. B Biol. Sci. *280*, 20123040.

Traveset, A., Tur, C., Trøjelsgaard, K., Heleno, R., Castro-Urgal, R., and Olesen, J.M. (2016). Global patterns of mainland and insular pollination networks: Mainland vs. insular pollination network structure. Glob. Ecol. Biogeogr. *25*, 880–890.

USDA, NRCS. 2019. The PLANTS Database (http://plants.usda.gov, 26 September 2019). National Plant Data Team, Greensboro, NC 27401-4901 USA.

Valtueña, F.J., Rodríguez-Riaño, T., López, J., Mayo, C., and Ortega-Olivencia, A. (2017). Peripatric speciation in an endemic Macaronesian plant after recent divergence from a widespread relative. PLOS ONE *12*, e0178459.

Vilà, M., Weber, E., and Antonio, C.M.D. (2000). Conservation Implications of Invasion by Plant Hybridization. Biol. Invasions *2*, 207–217.

Wallace, L.E., Culley, T.M., Weller, S.G., Sakai, A.K., Kuenzi, A., Roy, T., Wagner, W.L., and Nepokroeff, M. (2011). Asymmetrical Gene Flow in a Hybrid Zone of Hawaiian Schiedea (Caryophyllaceae) Species with Contrasting Mating Systems. PLoS ONE *6*, e24845.

Warren, B.H., Simberloff, D., Ricklefs, R.E., Aguilée, R., Condamine, F.L., Gravel, D., Morlon, H., Mouquet, N., Rosindell, J., Casquet, J., et al. (2015). Islands as model systems in ecology and evolution: prospects fifty years after MacArthur-Wilson. Ecol. Lett. *18*, 200–217.

Weigelt, P., Daniel Kissling, W., Kisel, Y., Fritz, S.A., Karger, D.N., Kessler, M., Lehtonen, S., Svenning, J.-C., and Kreft, H. (2015). Global patterns and drivers of phylogenetic structure in island floras. Sci. Rep. *5*, 12213.

Weller, S.G., Sakai, A.K., and Wagner, W.L. (2001). Artificial and Natural Hybridization in Schiedea and Alsinidendron (Caryophyllaceae: Alsinoideae): the Importance of Phylogeny, Genetic Divergence, Breeding System, and Population Size. Syst. Bot. *26*, 571–584.

Wendel, J.F., and Percy, R.G. (1990). Allozyme diversity and introgression in the Galapagos Islands endemic Gossypium darwinii and its relationship to continental G. barbadense. Biochem. Syst. Ecol. *18*, 517–528.

Whitney, K.D., Ahern, J.R., Campbell, L.G., Albert, L.P., and King, M.S. (2010). Patterns of hybridization in plants. Perspect. Plant Ecol. Evol. Syst. *12*, 175–182.

Whittaker, R.J. (1995). Disturbed island ecology. Trends Ecol. Evol. *10*, 421–425.

Whittaker, R.J., and Fernández-Palacios, J.M. (2007). Island biogeography: ecology, evolution, and conservation (Oxford ; New York: Oxford University Press).

Whittaker, R.J., Triantis, K.A., and Ladle, R.J. (2008). A general dynamic theory of oceanic island biogeography. J. Biogeogr. *35*, 977–994.

Wichman, S.R., Wright, S.D., Cameron, E.K., Keeling, D.J., and Gardner, R.C. (2002). Elevated genetic heterogeneity and Pleistocene climatic instability: inferences from nrDNA in New Zealand Coprosma (Rubiaceae). J. Biogeogr. *29*, 943–954.

Woodell, S.R.J. (1979). The Role of Unspecialized Pollinators in the Reproductive Success of Aldabran Plants. Philos. Trans. R. Soc. Lond. B. Biol. Sci. *286*, 99–108.

Yakimowski, S.B., and Rieseberg, L.H. (2014). The role of homoploid hybridization in evolution: A century of studies synthesizing genetics and ecology. Am. J. Bot. *101*, 1247–1258.