Is heterostyly rare on oceanic islands?

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Abstract. Heterostyly has been considered rare or absent on oceanic islands. However, there has been no comprehensive review on this issue. Is heterostyly truly rare on oceanic islands? What makes heterostyly rare on such islands? To answer these questions, we review the reproductive studies on heterostyly on oceanic islands, with special emphasis on the heterostylous genus *Psychotria* in the Pacific Ocean as a model system. Overall, not many reproductive studies have been performed on heterostylous species on oceanic islands. In Hawaiian *Psychotria*, all 11 species are thought to have evolved dioecy from distyly. In the West Pacific, three species on the oceanic Bonin and Lanyu Islands are distylos (Psychotria homalosperma, P. boninensis and P. cephalophora), whereas three species on the continental Ryukyu Islands show various breeding systems, such as distyly (P. serpens), dioecy (P. rubra) and monoecy (P. manillensis). On some other Pacific oceanic islands, possibilities of monomorphy have been reported. For many *Psychotria* species, breeding systems are unknown, although recent studies indicate that heterostylosus species may occur on some oceanic islands. A shift from heterostyly to other sexual systems may occur on some oceanic islands. This tendency may also contribute to the rarity of heterostyly, in addition to the difficulty in colonization/autochthonous evolution of heterostylous species on oceanic islands. Further investigation of reproductive systems of *Psychotria* on oceanic islands using robust phylogenetic frameworks would provide new insights into plant reproduction on oceanic islands.

Keywords: Dioecy; distyly; heterostyly; monoecy; oceanic islands; Pacific islands; *Psychotria*; reproductive system.

Introduction

Plant reproductive systems on islands have attracted the attention of many evolutionary biologists (Carlquist 1974; Ehrendorfer 1979; Bawa 1982; Baker and Cox 1984; Barrett et al. 1996; Sakai and Weller 1999; Crawford et al. 2011). Many general issues in evolutionary biology can be addressed using island plants (Barrett et al. 1996). Reproductive systems affect colonization, establishment, and maintenance and diversification of plants on islands (Carlquist 1974; Barrett et al. 1996; Crawford et al. 2011). Contradictions between strategies selecting for self-fertilization and cross-pollination have been one of the major issues for the reproductive studies of island plants (Barrett et al. 1996; Crawford et al. 2011). In an earlier study, Baker (1955) proposed that self-compatible, rather than self-incompatible, plants would be favoured in...
establishment after long-distance dispersal (later formulated as Baker’s Law (Stebbins 1957)); only one self-fertilizer is needed to reproduce after long-distance dispersal, while self-incompatible plants need at least two individuals. The paucity of pollinators on islands also enhances the advantages of self-compatible plants, because self-incompatible plants are more reliant on suitable pollinators to reproduce. Indeed, homomorphic or heteromorphic incompatible species are usually less common on oceanic islands than on continents (Barrett et al. 1996; Crawford et al. 2011).

In contrast, poor pollinator service resulting in selfing and inbreeding depression can cause the evolution of sexual dimorphism (Barrett et al. 1996). In fact, many major oceanic islands have a high proportion of dioecism (Carlquist 1974; Baker and Cox 1984; Sakai et al. 1995b; Abe 2006). Moreover, many examples of evolution of dimorphism from monomorphic ancestors are known from oceanic islands, such as the Hawaiian Islands (e.g. Bidens, Brassocasia, Cyrtandra, Hedvyotis, Neraudia, Santalum, Schiedea, Wikstroemia; Sakai et al. 1995b), the Bonin Islands (e.g. Callicarpa, Kawakubo 1990; Dendrocalacia, Kato and Nagamatsu 1995; Wikstroemia, Sugawara et al. 2004; Ligustrum, Tsuneki et al. 2011), the Mascarene islands (e.g. Chassalia, Pailier et al. 1998b; Dombeya, Humeau et al. 1999; Le Péchon et al. 2010), the Juan Fernandez Islands (Robinsonia, Bernardello et al. 2001) and the Canary Islands (Benconia, Marcetella, Helfgott et al. 2000; Withania, Anderson et al. 2006). Many studies of reproductive systems targeting island plants have focused on the occurrence and evolution of dioecism, but only a handful of studies have investigated the occurrence of heterostyly on oceanic islands.

Heterostyly is a genetically controlled floral polymorphism that promotes outbreeding (reviewed in Vuilleumier 1967; Ganders 1979b; Barrett 1992; Barrett and Shore 2008). It has attracted the attention of evolutionary researchers since Darwin (Darwin 1877; Weller 2009; Barrett 2010). Heterostyly includes distylly and tristyly, of which distylly is more common. A distylist population comprises two morphs: one is the short-styled morph (S-morph) with short styles and long anthers, and the other is the long-styled morph (L-morph) with long styles and short anthers. These two morphs usually have reciprocal positions in stigma and anther heights, and usually occur in equal numbers within a population. Distylist species usually possess an incompatibility system that prevents self-fertilization and intramorph fertilization (heteromorphic incompatibility). This herkogamous floral dimorphism is generally thought to be controlled by ‘a heterostylyous gene’ (Barrett and Shore 2008). In Primula, this heterostylyous gene is called as ‘a supergene’, which consists of three tightly linked diallelic genes (Charlesworth and Charlesworth 1979b; Lewis and Jones 1992).

It is generally thought that heterostyly is rare or absent on remote oceanic islands (Pailler et al. 1998b), despite the fact that outcrossing is advantageous for avoiding inbreeding depression (Barrett et al. 1996). Colonization is likely to be difficult for self-incompatible plants on oceanic islands and in situ evolution of heterostyly is almost impossible due to its complex genetic control system. Heterostyly may also be rare because it evolves into other breeding systems such as self-compatibility or dioecy, due to a paucity of suitable pollinators and a small population size on oceanic islands. Indeed, there are several examples of evolution of dioecy or self-fertilization from distyly on islands (e.g. Godley 1979; Beach and Bawa 1980; Pailler et al. 1998a). However, there has been no comprehensive review on this issue.

Given this background, we hypothesized that (i) heterostyly is truly rare on remote oceanic islands and (ii) this rarity is partly because of the tendency to shift from heterostyly to dioecism or self-fertilization on oceanic islands in addition to the difficulty in colonization/autochthonous evolution of heterostyly. One of the best ways to test these hypotheses is to compare reproductive systems of lineages distributed on oceanic and continental islands, and on continents using robust phylogenetic hypothesis. First, we briefly summarize the distribution of heterostylist plants on oceanic islands. Second, we document the breeding systems of the distylous genus Psychotria occurring on the Pacific islands as a model system for the study of heterostyly on islands. Finally, we discuss the reasons concerning the rarity and evolutionary modification of heterostyly on islands.

In this review, we focus on heterostyly on oceanic islands. We use the term ‘oceanic islands’ following Whittaker and Fernández-Palacios (2007) as ‘oceanic islands are those that have formed over oceanic plates and have never been connected to any continental landmass’. For this reason, the flora and fauna on oceanic islands are generally different from those of continental islands/fragments and continents (Carlquist 1974).

**Heterostyly on Oceanic Islands**

In earlier studies, it was often reported that heterostylist species were absent from oceanic island floras, e.g. Hawaii (Carlquist 1974) and Galapagos (McMullen 1987). Subsequently, Pailler et al. (1998b) considered that heterostyly may be absent or rare on oceanic islands. In general, it is very difficult to confirm whether heterostylist species are absent in particular islands because heterostyly is inconspicuous and often unnoticed in fields. In addition, the category of heterostyly or stylar polymorphisms has not been included in floristic surveys in many regions (e.g. Abe 2006; Tseng et al. 2008; Schlessman et al. 2014).

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Moreover, species with morphologically distyly flowers are sometimes functionally dioecious (e.g. *Mussaenda parviflora*, *Naik and Kato 1999*; *Psychotria rubra*, *Watanabe et al. 2014b*). Several recent studies indicate that heterostyly may be more common on oceanic islands than indicated by previous studies. Although the presence of heterostyly was not mentioned previously in the Galapagos Islands (*McMullen 1987*), two distyly species were recently reported: *Cordia lutea* (*McMullen 2012*) and *Waltheria ovata* (*Bramow et al. 2013*; Table 1).

Similarly, two *Psychotria* species endemic to the Bonin Islands were found to be distyly: *P. boninensis* (*Kondo et al. 2007; Sugawara et al. 2014*) and *P. homalosperma* (*Watanabe et al. 2014a*). On La Réunion Island of the Mascarene Islands, distyly in *Gaertnera vaginata* (*Pailler and Thompson 1997*) and three *Erythroxylum* species (*Pailler et al. 1998b*), and tristyly in *Hugonia serrata* (*Thompson et al. 1996; Meeus et al. 2011*) have been reported. In the Canary Islands, *Olesen et al. 2003* reported *Jasminum odoratissimum* as the only example of distyly in the islands.

Several pantropical species occurring on islands are heterostyly. *Pemphis acidula*, a littoral woody plant of *Lythraceae* distributed widely on pantropical islands, is distyly at least on several Indian Ocean Islands (*Lewis 1975*). *Lewis and Rao (1971)* suggested that distyly in *P. acidula* had probably been derived from tristyly based on its floral features, although there is no evidence that the distyly evolved on the islands. Interestingly, *P. acidula* in Mauritius is monomorphic as a consequence of breakdown of distyly on the island (*Lewis and Rao 1971*). *Guettarda speciosa*, a littoral woody plant of *Rubiaceae* occurring on pantropical islands, also exhibits stylar dimorphism (*T. Sugawara*, unpubl. data). *Pemphis* (*Murray 1986*) and *Guettarda* (*Nakonishi 1988*) disperse their propagules via water flotation, and are widely distributed from eastern Africa to the Pacific. This may imply a high number of migrants among island groups, as in *Ipomoea* (*Miryeganeh et al. 2014*). If their seeds arrive on particular islands repeatedly, the colonization of heterostyly plants may be facilitated.

Few heterostyly species and few studies of their reproductive biology are known from oceanic islands, and thus heterostyly is probably rare in such areas, as suggested by *Pailler et al. (1998b)*. However, there may be more heterostyly species as yet unrecognized as indicated by recent discoveries in the Bonin and Galapagos Islands. Further investigations will be necessary to ascertain the occurrence of heterostyly on oceanic islands.

**Breeding Systems of the Genus Psychotria in the Pacific Islands**

*Psychotria* (*Rubiaceae*) is a large genus comprising more than 1800 woody species and occurs widely in tropical to subtropical regions of the world (*Soehmer 1977; Hamilton 1990; Nepokroeff et al. 1999; Davis et al. 2001; 2009*). Its ancestral breeding system is thought to be distyly (*Hamilton 1990*). This genus provides an excellent

### Table 1

| Region          | Island group     | Species                  | Family     | BS    | Literature |
|-----------------|------------------|--------------------------|------------|-------|------------|
| Pacific Ocean   | Bonin Islands    | *Psychotria boninensis*   | Rubiaceae  | Distyly | 1, 2       |
|                 |                  | *P. homalosperma*        | Rubiaceae  | Distyly | 3          |
|                 | Galapagos Islands| *Cordia lutea*           | Boraginaceae| Distyly | 4          |
|                 |                  | *Waltheria ovata*        | Sterculiaceae| Distyly | 5, 6       |
| Indian Ocean    | La Réunion Island| *Gaertnera vaginata*    | Rubiaceae  | Distyly | 7          |
| (Mascarene islands²) |                  | *Erythroxylum laurifolium* | Erythroxylaceae| Distyly | 8          |
|                 |                  | *E. sideroxyloides*     | Erythroxylaceae| Distyly | 8          |
|                 |                  | *E. hypericifolium*     | Erythroxylaceae| Distyly | 8          |
|                 |                  | *Hugonia serrata*       | Linaceae   | Tristyly | 9, 10      |
| Atlantic Ocean  | Canary Islands   | *Jasminum odoratissimum* | Oleaceae  | Distyly | 11         |
| Pacific and Indian Ocean |                  | *Pemphis acidula*       | Lythraceae | Distyly | 12         |

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1. According to *Pailler* (1997), 27 indigenous species (6 genera/5 families) in the Mascarene Islands possibly are heterostyly including 5 species shown in the table. Those species are: *Erythroxylum* 4 spp. (*Erythroxylaceae*); *Hugonia* 2 spp. (*Linaceae*); *Olax psittacorum* (*Olacaceae*); *Gaertnera* 14 spp., *Psathura* 3 spp., *Donais* 3 spp. (*Rubiaceae*). Although *Baker* (1953) reported pollen and stigma dimorphism in several *Limonium* species from the Canary Islands, there is no evidence that they are heterostyly. *Olesen et al. 2003* also stated that *Jasminum* is the only one distyly example in the islands. Thus, we excluded them from the table. 1. *Kondo et al. 2007*, 2. *Sugawara et al. 2014*, 3. *Watanabe et al. 2014b*, 4. *McMullen 2012*, 5. *Schofield 1989*, 6. *Bramow et al. 2013*, 7. *Pailler and Thompson 1997*, 8. *Pailler et al. 1998b*, 9. *Thompson et al. 1996*, 10. *Meeus et al. 2011*, 11. *Olesen et al. 2003*, 12. *Lewis 1975*.
opportunity to study distyly on islands, because (i) it contains the largest number of distyly species (at least 127 spp. or more), (ii) it occurs frequently on remote oceanic islands, (iii) it has speciated on many islands and (iv) it contains examples of dioecism derived from distyly. In the Pacific islands, more than 400 species have been reported so far (Table 2).

If heterostyly is truly rare on oceanic islands as we hypothesized, most of these *Psychotria* species on oceanic islands in the Pacific may have evolved into other breeding systems from distyly before or after their colonization. The genus *Psychotria* is known as a ‘hyper-diversified woody genus’ in the tropics (Sedio et al. 2013). For example, only two colonists diversified into 81 species in New Caledonia (Barrábé et al. 2014), and a single colonist into 11 species in Hawaii (Table 2) (Nepokroeff et al. 2003). High species diversification is also found in the Philippines (95 species; Sohmer and Davis 2007), Fiji (76 species; Smith 1988), Papua New Guinea and the Bismarck Islands (115 species; Sohmer 1988), Marquesas (13 from three species; Lorence and Wagner 2005), etc. Despite the species diversity in each island, most species have never been studied from a reproductive perspective. According to Naiki (2012), *Psychotria* contains at least 127 distyly species, second only to *Primula* (Primulaceae) with 134 species in the number of species. Although only 127 out of 1800 *Psychotria* species are confirmed to be distyly, most of the other species yet to be studied are also considered to be distyly (Hamilton 1990). Thus the true number of distyly species in *Psychotria* should be much more, and probably

| Region                        | Area                | No. of species | Literature                                           |
|-------------------------------|---------------------|----------------|------------------------------------------------------|
| Continental East Asia         | China               | 16             | Tao and Taylor (2011)                                |
|                               | French Indo-China   | 26             | Pitard (1907)                                        |
| Eastern Asia-Pacific Islands  | ML Japan            | 1              | Yamazaki (1993)                                      |
|                               | Bonin Islands (Japan)| 2             | Toyoda (2003)                                        |
|                               | Ryukyu Islands (Japan)| 3           | Yamazaki (1993)                                      |
|                               | Taiwan              | 4              | Yang (1998)                                          |
|                               | Philippines         | 95             | Sohmer and Davis (2007)                              |
|                               | Irian Jaya          | 80 to 200      | Sohmer (1988)                                        |
|                               | Papua NG/Bismark    | 115            | Sohmer (1988), Takeuchi (2007)                       |
|                               | Mariana Islands     | 4              | Wagner et al. (2012) (Smithsonian website)           |
|                               | Caroline Islands    | 15             | Wagner et al. (2012) (Smithsonian website)           |
|                               | Australia           | 16             | Australian Plant Name Index (2015)                   |
|                               | New Zealand         | 0              | Moore and Edgar (1970)                               |
|                               | New Caledonia       | 81             | Barrábé et al. (2014), Barrábé (2014)               |
|                               | Fiji                | 76             | Smith (1988)                                         |
|                               | Tonga               | 5              | Yuncker (1959)                                       |
|                               | Samoa               | 20             | Whistler (1986)                                      |
|                               | Marquesas Islands (FP) | 13         | Lorence and Wagner (2005), Wagner and Lorence (2002) (Smithsonian website) |
|                               | Society Islands (FP)| 11             | Meyer et al. (2003)                                  |
|                               | Australes Islands (FP)| 3            | Meyer et al. (2003)                                  |
|                               | Hawai’i Islands      | 11             | Sohmer (1978), Wagner et al. (1999), Wagner et al. (2005) (Smithsonian website) |
|                               | Galapagos Islands   | 2              | Tye and Francisco-Ortega (2011)                      |
|                               | Juan Fernandez Islands | 0           | Marticorena et al. (1998), Danton et al. (2006), Bernardello et al. (2006) |
|                               | Easter Island       | 1²             | Orliac and Orliac (2008), Dubois et al. (2013)       |
|                               | Neotropics          | 208            | Sedio et al. (2013)                                  |

Table 2. Species number of *Psychotria* in East Asia, Pacific Islands and neotropics. There are at least still several undescribed *Psychotria* species (I. Meyer, pers. comm.) in the Pacific Ocean, and some other genera (e.g. Hydnophytwum, Amaracarpus, Dolianthus, Calycosia, Squamellaria) are thought to be included within the genus *Psychotria* (Barrábé et al. 2014; Razafimandimbison et al. 2014). On the other hand, ~20 species from the Pacific will be transferred to the genus *Margaritopsis* sect. Palicoureeae (Barrábé et al. 2012). Thus the species number shown here is just an estimate. ²Estimated extinct species.
this genus contains the most distyly species. Breakdown of distyly into monomorphy is frequently observed in the species occurring in the neotropics (Hamilton 1989, 1990; Sakai and Wright 2008), and evolution of dioecy from distyly has been also recognized in the Hawaiian Psychotria species (Sohmer 1977; Beach and Bawa 1980; Muenchow and Grebus 1989; Sakai et al. 1995b) and P. rubra in the Ryukyu Islands (Watanabe et al. 2014b).

Although genus-wide studies on reproductive biology of Psychotria have not been performed, the number of reproductive and molecular phylogeographic studies on Psychotria in the neotropics has increased during the past several decades (e.g. Hamilton 1989, 1990; Stone 1995, 1996; Almeida and Alves 2000; Faiivre and McDade 2001; Castro and Oliveira 2002; Castro and Araujo 2004; Castro et al. 2004; Coelho and Barbosa 2004, Rossi et al. 2005; Virillo et al. 2007; Sakai and Wright 2008; Souza et al. 2008; Consolaro et al. 2011; Faria et al. 2012). Several species, such as P. brachiatte, P. graciliflora, P. micrantha (Sakai and Wright 2008), P. carthagenensis (Consolaro et al. 2011; Faria et al. 2012), show both distyly and monomorphy in different populations. However, no example of transition from distyly to dioecy has been discovered in the neotropics.

In contrast to neotropical species, only a few reproductive studies have been reported in other areas, including Africa (Baker 1958), Indonesia (Ernst 1932), Hawaii (Sohmer 1977) and East Asia (Kondo et al. 2007; Sugawara et al. 2013, 2014; Watanabe et al. 2014a, b, 2015). Hawaiian Psychotria is one of the well-known examples of dioecy derived from distyly (Vuilleumier 1967; Beach and Bawa 1980; Muenchow and Grebus 1989; Barrett 1992). In the Hawaiian Islands, all 11 Psychotria species form a monophyletic group (Nepokroeff et al. 2003), and it has been believed that they are probably derived from a distyly colonist (Beach and Bawa 1980; Sakai et al. 1995b), since distyly is basal for the genus (Sohmer 1978). This modification has contributed to a high proportion of dioecism and low proportion of distyly on oceanic islands. However, there has been no direct evidence that the single colonist of Hawaiian Psychotria is distylos, because the closest sister species and its breeding system are still unclear. Moreover, although both dioecism and distyly promote outcrossing, selection against selfing or inbreeding depression cannot be a driving force of this evolution (Bawa 1980). To understand the evolutionary pathway of dioecism in Hawaiian Psychotria, more precise investigations on reproductive system and phylogenetic relationship among the related species are required.

In the western Pacific, six Psychotria species occur on the Bonin (Ogasawara) Islands, the Ryukyu Islands and Lanyu (Orchid) Island. The volcanic oceanic Bonin Islands consist of ~50 islands located ~1000 km south of the Japanese mainland, while the continental Ryukyu Islands include ~200 islands scattered between Taiwan and the Japanese mainland (Fig. 1). The Ryukyu Islands and Taiwan once were a part of the Chinese continent. Volcanic oceanic Lanyu Island is located off the southeastern coast of Taiwan (~60 km), but it has never been connected to the mainland of Taiwan or other landmass (Fig. 1). Our preliminary phylogenetic study, following Razafimandimbison et al. (2014), suggested that six Psychotria species in the Bonin and the Ryukyu Islands and Lanyu Island are divided into three lineages (Fig. 4).

We expected that Psychotria species on the oceanic islands would have dioecy or self-fertility derived from distyly, while the species on the continental islands maintain functional distyly. However, the results from current field investigations are contradictory to our hypotheses; all three species on the oceanic island (P. homalosperma and P. boninensis, both endemic to the Bonin Islands, and P. cephalophora on the Lanyu Island; Fig. 1) are distylos, while the other three species in the continental Ryukyu Islands show various breeding systems including distyly (P. serpens), dioecy (P. rubra) and monoecy (P. manillensis; Figs 2 and 3; Table 3). Psychotria homalosperma and P. boninensis are the
first example of distyly on the oceanic Bonin Islands. Functional dioecy in *P. rubra* is the second example in the genus, following Hawaiian species. Monoecism in *P. manillensis* is a unique example, because there has been no report of monoecism in distylos species groups (Naiki 2012).

Why has distyly been maintained or not on the islands, and dioecy/monoecy have been evolved? And now, we present some characteristics of the breeding system for several species of *Psychotria* obtained from our studies.

*Psychotria homalosperma*, an endemic and endangered tree (up to 12 m), is distylos with self-incompatibility (Watanabe et al. 2014a). Its flowers are white, long and narrow tubular with strong floral scent that contains large proportion of linalool (K. Watanabe, unpubl. data). Based on these features, we suppose that this species is adapted to hawkmoth pollinators. In the Bonin Islands, however, anthropogenic disruption of the insect fauna has been reported (Kato et al. 1999; Abe 2006; Abe et al. 2008). In our field investigations, the main flower visitor is an introduced honeybee (*Apis mellifera*), and moth visitation was recorded only once in more than 100 h of observations (Watanabe et al. 2014a; K. Watanabe, unpubl. data). This fact suggests that the shift of pollinators from long- to short-tongued insects, caused by human activity, may have occurred in this species on the oceanic Bonin Islands. This pollinator shift would result in unidirectional pollen flow from the S- to L-morphs (Fig. 5). In fact, the L-morph sets fruit 1.7–38 times more than the S-morph in the field (K. Watanabe, unpubl. data).

**Figure 2.** Inflorescences and fruit of six *Psychotria* species on the islands of Japan and Taiwan. Inflorescences and flowers (A) of *P. homalosperma* endemic to the Bonin Islands. Short- (B) and long-styled (C) flowers and fruit (F) of *P. cephalophora* on Lanyu Island. Short- (D) and long-styled (E) flowers of *P. boninensis* endemic to the Bonin Islands. Fruit (G) of *P. manillensis*, fruit (H) of *P. rubra* and fruit (I) of *P. serpens*, all in the Ryukyu Islands.
This difference is so large that it cannot be explained solely by S-biased sex ratios (1.5–3.5) in the field (Watanabe et al. 2014a). If this situation continues, the S-morph would supply only pollen grains like a male plant and the L-morph would receive them like a female plant. Eventually, \textit{P. homalosperma} may evolve into dioecy under this situation. However, \textit{P. homalosperma} has not regenerated recently, probably because of seed predation by introduced rats and deforestation (Watanabe et al. 2009).

\textit{Psychotria serpens}, a woody climber, is basically distyloous in the Ryukyu Islands, but the short homostyloous morph, together with the S- and L-morphs, is occasionally found in a population on Okinawa Islands (Sugawara et al. 2013). According to Sugawara et al. (2013), this homostyly is a consequence of unusual development of filaments and stamen. Therefore, the homostyloous plants occasionally found on the Okinawa Island may be exceptional for the species. According to the molecular
Table 3. Breeding systems of six *Psychotria* species occurring in Islands of Japan and Taiwan, and other examples of distylous species on remote oceanic islands. Oc, oceanic islands; Con, continental islands; S, short-styled; L, long-styled; Homo, homostyly; nd, no data. Ref., references; 1. Watanabe et al. (2014b), 2. Kondo et al. (2007), 3. Sugawara et al. (2014), 4. Sugawara et al. (2013), 5. Watanabe et al. (2014a), 6. Watanabe et al. (2015), 7. Mcmullen (2012), 8. Bramow et al. (2013), 9. Philipp et al. (2006), 10. Pailler and Thompson (1997), 11. Pailler (1998b), 12. Thompson et al. (1996), 13. Meesus et al. (2011), 14. Olesen et al. (2003), 15. K. Watanabe and T. Sugawara (unpubl. data).

**P<0.001; *P<0.01; NS, not significantly different = P > 0.05 after binomial test.**

| Island group | Species      | Ref. | Breeding system | Morphs | No. of pop. examined | Morph | Compatibility | Fruit set after hand pollination (%) | Pollination | Open fruit set (%) | Pollinator |
|--------------|--------------|------|-----------------|--------|----------------------|-------|---------------|-------------------------------------|-------------|-------------------|------------|
|              |              |      |                 |        |                      |       |               |                                      |             |                   |            |
| Bonin Islands (Oc) |              |      |                 |        |                      |       |               |                                      |             |                   |            |
| P. homalosperma | 1, 15 Distyly | S, L | 3 | 1.5–2.3 | ** | SI, LL, SS³ | 82.4 | 82.6 | 0 | 0 | 5.9 | 0 | 2.8–8.9 | 0.2–1.4 | Bee (moth) |
| P. boninensis | 2, 3 Distyly | S, L | 1 | 1.05 | NS | SI, LL, SS | 7.1 | 27.6 | 0 | 0 | 0 | 0 | 12.6; 18.6 | 9.2; 8.4 | Bee (bee) |
| Ryukyu Islands (Con) |              |      |                 |        |                      |       |               |                                      |             |                   |            |
| P. serpens | 4, 15 Distyly | S, L, Homo | 3 | nd | - | SI, LL, SS³ | 78.9 | 85.0 | 0 | 0 | 6.3 | 0 | 53.4 | 40.2 | Bee, Wasp |
| P. rubra | 5 Dioecy | Male, Female | 4 | 1.3–2.0 | ** | - | - | 0 | 64.9 | - | - | - | - | 40.5 | 0 | Fly, Wasp |
| P. manillensis | 15 Monoecy | Herm, Female | 5 | - | - | SC | - | - | - | - | - | - | - | 11.9 | N | Fly, Wasp |
| Lanyu Island (Oc) |              |      |                 |        |                      |       |               |                                      |             |                   |            |
| P. cephalophora | 6 Distyly | S, L | 1 | 1.0 | NS | SI, LL¹, SS | 100² | 100² | 0² | 0² | 3.3² | 0² | 5² | nd | nd | Moth, beetle? |
| Galapagos (Oc) |              |      |                 |        |                      |       |               |                                      |             |                   |            |
| C. lutea | 7 Distyly | S, L | 1 | nd | - | SC¹ | LL, SS | 74³ | 25³ | 9³ | 20³ | 54⁴ | 75⁴ | Beetle, bee |
| W. ovate | 8, 9 Distyly | S, L | 12 | 1.33–0.56 | SC¹ | LL, SS | 68⁵ | 61⁵ | 20⁵ | 60⁵ | 21⁴ | 4⁴ | 54⁴ | 75⁴ | Bee, fly, grasshopper |
| La Reunion (Oc) |              |      |                 |        |                      |       |               |                                      |             |                   |            |
| G. vaginata | 10 Distyly | S, L | 18 | 0.75–1.82 | * | SI, LL, SS³ | 92.2 | 92.8 | 0 | 0 | 19.4 | 0 | 29–49 | 21–39 | nd |
| E. laurifolium | 11 Distyly | S, L | 3 | 0.78–1.44 | NS | SI, LL¹, SS | 72.4 | 69.8 | 1.6 | 3.1 | 2.0 | 12.8 | nd | nd | Moth? |
| E. sideroxylonides | 11 Distyly | S, L | 1 | nd | nd | nd | nd | nd | nd | nd | nd | nd | nd | nd | nd |
| E. hypericifolium | 11 Distyly | S, L | 1 | nd | nd | nd | nd | nd | nd | nd | nd | nd | nd | nd | nd |
| H. serrata | 12, 13 Tristyly | S, M, L | 1 | 1S: 3M: 5L | - | SI | nd | 66.³⁶⁴⁶ | 3.6³⁶⁴⁶ | nd | nd | S: 27³⁶, M: 43³⁶, L: 44³⁶ | Bee (butterfly?) |
| Canary Islands (Oc) |              |      |                 |        |                      |       |               |                                      |             |                   |            |
| J. odoratissimum | 14 Distyly | S, L | 2 | 0.91; 1.54 | NS | nd | nd | nd | nd | nd | nd | nd | nd | nd | nd |
Phylogenetic data (Fig. 4), *P. boninensis*, a woody climber endemic to the Bonin Islands, is supposed to be derived from *P. serpens*. Thus the ancestral colonist of *P. boninensis* on the Bonin Islands also appears to be distyloous.

*Psychotria rubra*, a shrub of non-limestone broad-leaved forests in the Ryukyu Islands is morphologically distyloous with L- and S-morphs (Watanabe et al. 2014b). However, the S-morph never set any fruit, whereas the L-morph never had pollen grains (Watanabe et al. 2014b). Therefore, this species is functionally dioecious. Considering the morphological features, the dioecy found in *P. rubra* is probably derived from distyly. To discuss the evolutionary pathway of dioecy in *P. rubra*, we need to compare precise reproductive systems among the closely related species with a reliable phylogenetic tree.

*Psychotria manillensis*, a shrub of limestone broad-leaved forests in the Ryukyu Islands, is monoecious and self-compatible (Table 3) (K. Watanabe, unpubl. data). This reproductive system is particularly interesting, because no other monoecism has been found in other distyloous species groups in flowering plants. Theoretically, it is very difficult to explain the evolution of monoecism from distyly because distyly is a genetically controlled dimorphism. Although the detailed phylogenetic relationships among the species are still unsolved, *P. manillensis* is closely allied to *P. rubra* based on morphology and preliminary molecular data (Fig. 4). Cytologically, *P. manillensis* is octoploid (2*n* = 84), while *P. rubra* is tetraploid (2*n* = 42) (Nakamura et al. 2003). These chromosomal data suggest that *P. manillensis* may be a polyploid derivative of *P. rubra*. If the genes responsible for sexual determination of flowers became heterogeneous through doubling of chromosomes, the plant can have both male and female flowers within a single plant (monoecy).

Reproduction and Evolutionary Modification of Heterostyly on Islands

What makes heterostyly rare in floras of isolated islands? Three possible reasons can be raised for its rarity on...
Islands: (i) failure of colonization, (ii) difficulty in autochthonous evolution of distyly and (iii) the evolutionary modification into other breeding systems such as self-compatibility, dioecism, monoeism.

Failure of colonization should be mostly due to self-incompatibility of heterostyly species (Pailler et al. 1998b). It is surely difficult for self-incompatible species to reproduce on islands compared with self-compatible species, as mentioned by Baker (1955). However, the rarity of heterostyly on islands may not be explained only by this reason, because many dioecious colonists are known from oceanic islands. In fact, almost one-third of the extant dioecious species in the Hawaiian Islands are derived from dioecious ancestors (Sakai et al. 1995b). Although heterostyly is much less common than dioecy even in mainland areas, some heterostyly plants may reach the remote oceanic islands.

Colonization of oceanic islands by reproductively dimorphic plants is often associated with bird dispersal (Bawa 1980; Lloyd 1985; Sakai et al. 1995a; Webb et al. 1999). One of the reasons for this may be because clumped dispersal of propagules facilitates colonization of dimorphic plants (Sakai et al. 1995a). Of 11 heterostyly species that occur on oceanic islands (Table 1), 9 (Cordia, Erythroxylum, Gaertnera, Hugonia, Jasminum and Psychotria) have fleshy fruits, and at least four of them have seeds dispersed by birds (Psychotria, Ono and Sugawara 1981; Cordia, Heleno et al. 2011; Gaertnera, Malcomber 2002). Their colonists are presumably dispersed by birds, like dioecious colonists in other oceanic islands. On the other hand, Waltheria (Carququist 1974), Pemphis (Murray 1986) and Guettarda (Nakanishi 1988) have sea-drifted seeds, and this mode of dispersal may also be related to their colonization.

Of 11 heterostyly species occurring on oceanic islands (Table 1), six species (P. homalosperma, P. boninensis, P. cephalophora, Gaertnera vafinata, Erythroxylum laurifolim and H. serrata) are basically self-incompatible (Table 3), although P. cephalophora and E. laurifolium are slightly self-compatible. This fact suggests that multiple ancestors may have colonized the islands. Cordia and Waltheria in the Galapagos Islands show partial self-compatibility, known as ‘leaky incompatibility’ (McMullen 2012; Bramow et al. 2013). This leaky self-incompatibility might help their initial colonization and spread among islands in the Galapagos. It is notable that all 11 species are long-lived woods, and their colonists might survive long enough for conspecifics to colonize (Meeus et al. 2011).

Because heterostyly plants require pollinators suitable for their reproduction, the heterostyly species on oceanic islands provide evidence that continuous pollinator services exist on islands. This stable pollinator services might be unusual for oceanic islands, where ecosystems are usually unstable (Abe 2006).

Geography is also important for understanding colonization and reproduction of heterostyly species on oceanic islands. Watanabe et al. (2015) reported distyly in P. cephalophora from oceanic Lanyu Island, which is only 60 km away from the south of Taiwan, but has never been connected to it. There seems to be several more distyly plant species on the island (K. Watanabe, pers. obs.). Many floristic elements are shared between Lanyu Island and other northern islands in the Philippines where P. cephalophora occurs (Nakamura et al. 2014). Psychotria cephalophora might have colonized Lanyu Island repeatedly, since it is located near the big continental islands, unlike more remote oceanic islands. Moreover, ~700 native plant species occur on Lanyu Island (50 km² in area) (Tseng et al. 2008), which is more than twice as many species as in the Bonin Islands (~70 km²) (Toyoda 2003). This environment with rich species probably supports the reproduction and maintenance of heterostyly species on oceanic Lanyu Island.

Some remote oceanic islands, like the Hawaiian and the Bonin Islands (5000 and 1000 km from the nearest continent or continental islands, respectively), are quite isolated from any other landmass, while some other oceanic islands close to the mainland, like Lanyu Island and Izu-Oshima Islands (20 km from mainland Japan),
are largely affected by continental biota. We need to take these geographical and historical conditions into account to understand how heterostyly species colonize and reproduce on oceanic islands.

The rarity of heterostyly on islands may also result from the difficulty in autochthonous evolution of heterostyly on islands. Outcrossing is advantageous for island plants, and it may drive monomorphic plants to evolve dioecy within islands (in situ evolution) because dioecy is easily established (Baker and Cox 1984). Indeed, there are many examples of in situ evolution of dioecism on islands (e.g. Sakai et al. 1995b; Baker and Cox 1984). Compared with establishment of dioecy, however, the establishment of heterostyly is far more difficult (Carlquist 1974), because of the complexity of the genetic control of heterostyly (Lewis and Jones 1992).

The paucity and bias of pollinator fauna and small population sizes on islands may cause the evolutionary modification of heterostyly into other breeding systems. The breakdown of heterostyly into monomorphy can be caused by recombination within ‘a heterostylyous gene’ (Charlesworth and Charlesworth 1979a; Washitani 1996), but this recombinant cannot spread in natural populations under a stable environment because distyly is an efficient mechanism to avoid inbreeding depression (Charlesworth and Charlesworth 1979a). However, the recombinants would spread when suitable pollinators decline or the population size is decreased (Washitani et al. 1994; Washitani 1996).

Low availability of pollinators and small plant population sizes are the characteristic features on oceanic islands. Thus, the evolutionary breakdown of heterostyly can be caused more frequently on oceanic islands than on continents, which may contribute to the rarity of heterostyly on islands. Recently, Lorence and Wagner (2005) reported that flowers of many Psychotria species in the Marquesas appeared to be homostylos. Of course more precise observations and experiments are needed to confirm their functional breeding systems and evolutionary pathways, but there may be a number of Psychotria species having undetected homostyly in the Pacific.

In the Caribbean Islands, although they are not oceanic islands but continental fragments, several interesting evolutionary modifications of heterostyly have been reported (reviewed in Barrett et al. 1996). Self-compatible, tristylos Eichhornia paniculata lost one of its morphs on Jamaica, probably because of poor pollinator services (Barrett et al. 1996). A similar example was reported from Turnera ulmifolia, of which more self-compatible homostylosus and fewer self-incompatible distylosus varieties were found on small islands in contrast to continents (Barrett and Shore 1987).

Evolution of dioecy from distyly is found much less frequently than the evolution of self-fertilization is (Barrett and Richards 1990). Muenchow and Grebus (1989) listed eight genera as possible examples of this pattern. We revised this list in Table 4 based on the recent literature; 3 of 10 genera listed in Table 4 may have occurred on islands.

Several hypotheses may account for the evolution from distyly to dioecy (e.g. Ornduff 1966; Beach and Bawa 1980; Webb 1999; Rosas and Dominguez 2009). Beach and Bawa (1980), following Robertson (1892) and Baker (1958), proposed that the unidirectional (one-way) pollen flow from S- to L-morphs leads to separate sexes.

### Table 4. Examples of the plants evolved from distyly to dioecy. 1Including dioecious genera within genus Guettarda.

| Family        | Genus       | Location         | Literature                                      |
|---------------|-------------|------------------|------------------------------------------------|
| Rubiaceae     | Chassalia   | La Reunion        | Pailler et al. (1998a)                          |
|               | Coussarea   | Costa Rica       | Beach and Bawa (1980)                          |
|               | Goertnera   | Paleotropics     | Van Beusekom (1967), Malcomber (2002), Malcomber and Taylor (2009) |
|               | Guettarda (Timonius/Antirhea) | Worldwide | Achille et al. (2006) (Guettarda), Litrico et al. (2005) (Antirhea) |
|               | Mussaenda   | Asia              | Baker (1958), Nolki and Kato (1999)             |
|               | Psychotria  | Hawaiian Islands | Vuilleumier (1967), Sohmer (1977), Hamilton (1990) |
|               | Phyllopetas | Madagascar       | Andriamihajarivo et al. (2011)                  |
| Boraginaceae  | Cordia      | Costa Rica       | Opler et al. (1975)                            |
| Menyanthaceae | Nymphoides  | North America    | Ornduff (1966)                                 |
| Elthyroxylaceae | Etyroxylum | Costa Rica       | Bowa and Opler (1975), Ganders (1979a), Abarca et al. (2008) |
A pollinator shift from long- to short-tongued pollinators initiates unidirectional pollen flow from S- to L-morphs (Fig. 5), resulting in the L-morph becoming male-sterile (Beach and Bawa 1980). It eventually drives the evolution of the breeding system from distyly to dioecy. Muenchow and Grebus (1989) suggested that the complete disappearance of the long-tongued pollinators at the initial stage and the male sterility of the L-morph were required for the scenario. A change of pollinators could occur on oceanic islands too, since the pollinator fauna is usually poorer on oceanic islands than on continents (Barrett et al. 1996). For example, a distylosous plant whose original pollinator is a long-tongued hawkmoth would experience a complete pollinator shift from long- to short-tongued pollinators following colonization of an island where only short-tongued insects are available. Psychotria homalosperma, which has functional distyly on the Bonin Islands, may show the initial stage of this transition.

Polyploidization and hybridization are assumed to have played an important role in the evolution of several taxa in the Hawaiian Islands (reviewed in Keeley and Funk 2011). These phenomena may have also driven the evolution of breeding systems on other islands. Recently, a correlation between breakdown of distyly and polyploidy has been recognized in several taxa (Damnacanthus, Naiki and Nagamasu 2004; Turnera, Shore et al. 2006; Ophiarrhiza, Nakamura et al. 2007). Later, Naiki (2012) concluded in his review of a wide range of taxa across the world that polyploidy was not always accompanied with the breakdown of distyly, but that following the breakdown of distyly, polyploidy in monomorphic plants could decrease the expression of inbreeding depression. Although the process of evolution of monoecy in octoploid Psychotria manillensis still remains unclear, genetic recombination or chromosomal doubling may be involved in the evolution of its unusual breeding system.

**Future Prospects**

Heterosty on remote islands provides an opportunity to deepen our understanding of plant reproductive biology. We propose the following three steps in future investigations. First, we need comparative studies within lineages to investigate breeding systems of island species and their closest continental relatives. Although few heterostylyous lineages occur on islands, genera such as Psychotria provide excellent opportunities for analysis of evolutionary modifications of heterostely associated with colonization of oceanic islands. To understand the reproductive system of each species, a study should include not only its floral traits, but also its functional breeding system, incompatibility, open fruit set, plant–pollinator interactions and pollen flow. Second, we need to construct a robust phylogenetic framework to trace the evolutionary pathway of each species with high confidence. Third, we also need to consider the environmental and historical background of islands. The simple classification into ‘oceanic’ or ‘continental’ islands might not be enough to explain the ecological background. Instead, careful examinations of correlations between breeding systems and geographical/historical conditions are needed to understand the general patterns of heterostely on islands.

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**Contributions by the Authors**

K.W. and T.S. contributed to writing of the paper.

**Conflict of Interest Statement**

None declared.

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