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A comparison of reproductive strategies between island and mainland Caribbean Gesneriaceae

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Summary

1. The evolution of self-pollination has long been considered an adaptive strategy to cope with low or variable pollinator service; however, alternative reproductive strategies, such as generalized pollination (>1 pollinator functional group), may also ensure plant reproductive success in environments with inadequate pollinator visitation.

2. Island–mainland systems provide ideal settings to assess the interaction between pollination and breeding systems in response to pollinator visitation because islands are often pollinator-depauperate. This study compared 28 insular and 26 mainland species of Caribbean Gesneriaceae to test the hypothesis that low diversity and possibly low pollinator service on islands would lead to a greater frequency of generalized plant–pollinator interactions and/or a higher potential for autonomous self-pollination in insular than in mainland species. We also assessed the hypothesis that epiphytic species should have greater autofertility than species occurring in other habitats.

3. Pollinator observations conducted in the field from 2004 to 2014 revealed bat, bee, butterfly, hummingbird, moth, and generalized pollination systems. Functional specialization in pollination systems was high in insular (71% of the species) and mainland sites (all species), but generalized and bat-pollinated species were more common on islands. Overall, pollinator visitation rates did not differ between island and mainland; however, for hummingbird-pollinated species, visitation rate was on average three times higher in mainland than island species. Autofertility indices (fruit set of bagged/outcross flowers) ranged from 0 to 1 and did not differ between island and mainland species. Species growing on rocks (rupiculous) and trees (epiphytic) had on average higher autofertility than terrestrial species.

4. *Synthesis.* This study revealed that alternative reproductive strategies are used in pollinator-depauperate environments. Pollinator visitation is lower in insular hummingbird-pollinated species (the ancestral pollination system of insular Gesneriaceae); therefore, generalized pollination may be considered a reproductive assurance mechanism evolved primarily on island environments. Contrary to the long-standing tenet, however, autonomous self-pollination was similar in island and mainland Gesneriaceae suggesting that: (i) generalized pollination provides a viable alternative to selfing in pollinator-depauperate environments, (ii) autofertility as a reproductive assurance mechanism may be frequent in plant species from mainland regions in environments with unpredictable pollinator visitation and resource availability.

Key-words: Caribbean, Gesneriaceae, island, mainland, pollination, reproductive ecology, self-pollination, specialization

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Introduction

Islands generally have depauperate faunas with a poor representation of some animal pollinator groups (Carlquist 1974; Barrett, Emerson & Mallet 1996). For example, long-tongued lepidopterans and social bees are often rare in oceanic islands, while flies are common floral visitors (McMullen 1987; Inoue 1993; Newstrom & Robertson 2005). The ecological and evolutionary consequences of this reduced pollinator diversity partly depend on the pollination and breeding system of each plant species. For instance, vulnerability to pollination failure should be greater in species with obligate outcrossing breeding systems and specialized pollination systems (e.g. one–few pollinator species, a.k.a., ecological specialization, Armbruster, Fenster & Dudash 2000; one functional group of pollinators with common behaviours and morphologies exerting similar selection on flowers, a.k.a., functional specialization, Fenster *et al.* 2004). Thus, evolutionary transitions in response to limited pollinator visitation are expected in insular plant lineages, with shifts to novel specialized pollination systems (e.g. pollination by crickets in *Angraecum*, Micheneau *et al.* 2010), or to generalized pollination systems (Armbruster & Baldwin 1998; Smith, Ané & Baum 2008; Martén-Rodríguez *et al.* 2010). Alternatively, natural selection may favour autonomous reproductive strategies in insular environments (Baker 1955).

The reproductive biology of island plants has been the focus of much research (García-Verdugo & Fay 2014). For instance, studies conducted on whole plant communities of remote oceanic islands show a high frequency of self-compatible species capable of autonomous self-pollination (Faroes, Hagerup 1951; Hawaii, Carlquist 1974; New Zealand, Lloyd 1985; Galapagos, McMullen 1987; San Juan Fernandez, Bernardello *et al.* 2001). However, these studies do not make direct comparisons to mainland communities. At the species level, there are few comparative studies on the reproductive ecology and evolution of plant lineages in mainland and island environments. In this context, the available evidence indicates that insular plant populations tend to have more generalized pollination systems and lower pollinator visitation rates than their conspecifics in neighbouring mainland equivalents (e.g. Tobago and Trinidad, Spears 1987; Izu Islands and Japan, Inoue, Maki & Masuda 1996). Additionally, some studies have shown the breakdown of outcrossing systems such as the evolution of self-pollination in insular plant populations (Barrett 1985; Inoue, Maki & Masuda 1996; Bramow *et al.* 2013). For example, in a comparison of Brazilian and Jamaican populations of tristylous *Eichhornia paniculata*, Barrett (1985) determined that individuals of mainland origin presented the expected three floral morphs, whereas individuals of insular origin had exclusively mid-styled, self-pollinating flowers. These kinds of comparative studies provide a unique opportunity to study changes in breeding systems at a microevolutionary scale. Studies involving related species in mainland and island environments may similarly advance our understanding of the processes underlying evolutionary transitions in pollination and breeding systems across plant lineages.

The Neotropical Gesneriaceae (ca. 1200 spp.) provide a suitable study system to evaluate potential drivers of evolutionary change in plant reproductive strategies because it exhibits great floral diversity in both island and mainland environments. In the Mesoamerican region and Caribbean islands, there are approximately 400 species, of which some 75 species are restricted to the Antilles (Skog 1976; Tropicos.org. Missouri Botanical Garden. 19 Jan 2015, http://www.tropicos.org/Name/42000302?projectid=3&langid=66). Antillean Gesneriaceae form a clade that includes a variety of floral phenotypes associated with pollination by hummingbirds, bats, moths, bees or a combination of these animal groups (i.e. functionally generalized pollination systems, Martén-Rodríguez, Almarales-Castro & Fenster 2009; Martén-Rodríguez *et al.* 2010). Ancestral state reconstructions indicate that hummingbird pollination is ancestral in this insular clade, with at least two transitions to bat pollination and three transitions to generalized pollination (Martén-Rodríguez *et al.* 2010). In mainland Gesneriaceae, pollination systems are also diverse and inferences from comparative analyses suggest that transitions in floral syndromes are common (e.g. SanMartin-Gajardo & Sazima 2005; Wolowski *et al.* 2013). There is little information on the evolution of breeding systems of Neotropical Gesneriaceae, but there is evidence for widespread intrafloral dichogamy (i.e. the temporal separation of male and female phases) in both insular and mainland species (SanMartin-Gajardo & Sazima 2004; Martén-Rodríguez & Fenster 2008; Wolowski *et al.* 2013). Furthermore, some Gesneriaceae species are capable of autonomous self-pollination, a condition that appears to have evolved more than once in the Antilllean clade (Martén-Rodríguez *et al.* 2010). The frequency of species capable of delayed autonomous self-pollination in mainland regions has not yet been assessed.

We evaluated the hypothesis that low diversity and possibly low pollinator service on islands would be associated with the evolution of less specialized plant–pollinator interactions (Barrett, Emerson & Mallet 1996), and a greater frequency of autogamous breeding systems in insular than in mainland species (Baker 1955). We also examined the relationship between habitat condition and breeding system since these traits may not evolve independently. In particular, it has been suggested that the epiphytic habit may be associated with self-pollination in various groups of tropical plants (e.g. Gentry & Dodson 1987; Bush & Beach 1995; Benzing 2000). This has been related to the occurrence of epiphytes in unstable substrates (i.e. tree branches prone to breaking and falling), limited resources for reproduction, and dispersed spatial distributions (Benzing 1990; Bush & Beach 1995). These conditions may favour breeding strategies associated with the colonization of new habitats, such as self-compatibility and autonomous self-pollination, to ensure seed production under conditions of pollinator or mate scarcity (Cascante-Marín *et al.* 2006). While there is evidence for widespread self-compatibility in large plant families of primarily epiphytic species, for example orchids (Tremblay *et al.* 2005) and bromeliads

(Benzing 2000), there are no within-family assessments of the capacity for autonomous self-pollination in relation to habitat condition in these plant groups. The family Gesneriaceae includes species that may be epiphytic (i.e. growing on other plants), rupiculous (i.e. growing on rocks) or terrestrial. Thus, we considered habitat condition in Caribbean Gesneriaceae as a variable potentially associated with breeding system.

In this study, we documented pollinator visitation and autonomous self-pollination in a sample of Gesneriaceae species native to the insular and mainland Caribbean region. We expected that the low diversity of animal pollinators on islands would lead to lower pollinator visitation rates in insular than in mainland sites, conditions that would have favoured the evolution of less specialized pollination systems on islands. Alternatively, low diversity and abundance of pollen and nectar-feeding animal species may translate into more specialized pollination systems on islands. We also expected that the potential for autonomous self-pollination would be higher in insular than in mainland species and that epiphytic plants would have greater potential autofertility than species occurring in other habitats.

Materials and methods

STUDY SPECIES AND SAMPLING

We used a set of 54 species of Gesneriaceae that were studied in mainland Costa Rica and Mexico, and in the Caribbean islands between 2004 and 2014 (Table 1, Fig. 1). Mainland species belong to various tribes of the family Gesneriaceae, while insular species all belong to the Antillean clade Gesnerieae. The sampling included our own published data on 13 Caribbean species that had complete information for both pollinator visitation and autonomous self-pollination, and eight species that had information for pollinator visitation only (Martén-Rodríguez, Almarales-Castro & Fenster 2009; Martén-Rodríguez & Fenster 2010). The pollination and/or breeding systems of the remaining species were determined through field observations and experiments conducted between 2007 and 2014. We are confident that this data set is reliable because there was little variation in pollinator assemblages across years for species that were sampled on multiple years (50% of the species). We were able to obtain estimates of pollinator visitation and breeding systems for most species; however, we lack pollinator visitation data for five species and autofertility data for seven species (see Tables 1 and 3); these data could not be recorded for logistic and safety reasons. Study species include terrestrial, epiphytic or rupiculous herbs, shrubs and small trees that include a variety of floral phenotypes. These species have self-compatible breeding systems, with flowers that are generally dichogamous (showing temporal separation of male and female phases). Overlap of sexual phases within the flower allows for delayed autonomous self-pollination in various species. Self-pollination occurs when receptive stigmas come into contact with anthers containing pollen at the end of the flower′s life (Martén-Rodríguez & Fenster 2008, 2010).

STUDY SITES

Documentation of reproductive systems was conducted at various locations in continental Costa Rica and Mexico, and insular Cuba, Hispaniola, Jamaica, Puerto Rico and St. Lucia. All species were studied under natural conditions in their native populations. We selected field sites that had the least possible human disturbance, including National Parks, Biosphere Reserves and private reserves. We visited each site for 5–8 days at least twice during the study period and marked all flowering Gesneriaceae species found at each site. Specific site locations and GPS coordinates are provided in Appendix S1 (Supporting Information). Each Gesneriaceae species was sampled at a single study site.

The main pollinators of Neotropical Gesneriaceae include bats, bees and hummingbirds, but the species richness of these animal groups differs between island and mainland regions. The number of species of the major nectar and pollen-feeding animal groups in the study region indicates that insular sites have lower species richness than mainland sites (see Appendix S2).

POLLINATION SYSTEMS AND VISITATION RATES

We determined the pollination systems of each plant species using direct observation and video cameras (Sony Camcorders), for a total of 1083 observation hours. The number of hours and plants observed for each species are reported in Table 1. For analyses, we only included species with at least 8 h of pollinator observations and with more than one pollinator visit recorded. The number of observation hours was generally higher for species with nocturnal anthesis because these were only observed with video cameras that focus on one or few flowers at a time. We conducted observations for periods of 1–2 h, and for each visit, we recorded the identity of the floral visitor, the number of flowers probed on each visit, and whether or not there was contact with the reproductive organs of the flower. Whenever possible, we recorded pollen on pollinator's bodies from the videos. We recorded all floral visitors and noted their visitation frequency and behaviour. We counted all flowers observed on each individual plant and calculated visitation rates flower^{-1} h^{-1} considering only effective visitors (i.e. animals that contacted the flower′s reproductive organs (see Appendix S3).

For six species representing the floral syndromes that received visits by more than one functional group (chiropterophilous: *G. pedunculosa*, ornithophilous: *R. asperum,* mixed pollination syndrome: *G. viridiflora* subsp. *sintenisii*, *R. auriculatum, R. grandiflorum, R. vernicosum*), we assessed whether contact with the reproductive organs could be used as a proxy for efficiency to distinguish potential pollinators from non-pollinating visitors. This sample included 33% of the Gesneriaceae species that had two or more functional groups of floral visitors (*n* = 18 species, Table 1). We covered flower buds to prevent visitation and then exposed virgin flowers to natural visitation. These flowers were observed with video cameras as described above; at the end of each observation period, flowers were checked with an Eschenbach 10× hand lens. We coded each flower positive or negative for pollen deposition on stigmas and pollen removal from anthers. Contact with reproductive organs observed in the videos consistently corresponded with removal from anthers and/or deposition of pollen on stigmas, consistent with the findings of many other studies (Rosas-Guerrero *et al.* 2014). Since pollen deposition on stigmas is usually in the thousands and more quantitative measures of pollinator effectiveness are difficult to obtain for such a large group of species, we used contact with reproductive organs as an indicator of potential pollination by floral visitors. This method allowed us to consistently compare pollinator visitation across species occurring in

Table 1. Gesneriaceae species studied at various sites in Costa Rica, Mexico and the Antillean islands between 2004 and 2014. The codes that identify each species in Fig. 2 are listed and followed by habitat condition (HC coded as: E = epiphytic, R = rupiculous, T = terrestrial), country, functional group of pollinator or non-pollinating visitor, floral visitor identified to the lowest possible taxonomic level (in parenthesis *n* is the number of individuals observed), number of pollinator observation hours (in parenthesis is the number of plants observed), and study years

Species	Code	HC	Country	Pollinator/visitor functional group	Pollinator/visitor species	No. hours (plants)	Year
Mainland (*n* = 26)							
Achimenes antirrhina	Aa	R	Mexico	Hummingbird	*Amazilia beryllina* (*n* = 5)	22 (10)	2012–2014
Achimenes flava	Af	R	Mexico	Bee	Anthophoridae (*n* = 8, 2 spp.)	22 (50)	2012–2014
Achimenes obscura	Ao	R	Mexico	Bee	*Trigona fulviventris* (*n* = 6)	10 (30)	2012, 2014
Achimenes patens	Ap	R	Mexico	Butterfly	Unidentified (*n* = 7, 3 spp.)	22 (60)	2012–2014
Besleria columneoides	Bc	T	Costa Rica	Hummingbird	*Phaetornis longemareus* (*n* = 4)	15 (8)	2011, 1013
Besleria grandiflora	Bg	T	Costa Rica	Hummingbird	Unidentified sp. (*n* = 3).	12 (6)	2011
Besleria solanoides[‡]	Bs	T	Costa Rica	Hummingbird Butterfly*	*Lampornis calolaema* (*n* = 4) Unidentified sp. (*n* = 1)	19 (12)	2007, 2010
Besleria trichostegia	Bt	T	Costa Rica	Hummingbird	*Phaetornis longemareus* (*n* = 4)	18 (9)	2011
Chrysothemis friedrichsthaliana	Cf	T	Costa Rica	Hummingbird	*Amazilia tzacatl* (*n* = 3)	16 (8)	2010, 2013
Codonanthe crassifolia[†]	Cr	E	Costa Rica	Moth	Not observed	4 (4)	2013
Columnea consanguinea[‡]	Cc	E	Costa Rica	Hummingbird	*Heliodoxa jacula* (*n* = 3)	13 (5)	2007
Columnea linearis	Cl	E	Costa Rica	Hummingbird Stingless bee[§]	*Amazilia tzacatl* (*n* = 3) *Trigona* sp. (*n* = 2)	13 (7)	2011
Columnea magnifica	Cm	E	Costa Rica	Hummingbird	*Eugenes fulgens* (*n* = 4)	12 (5)	2010
Columnea nicaraguensis	Cn	E	Costa Rica	Hummingbird Stingless bee[§]	*Heliotrix barrotii* (*n* = 4), *Amazilia tzacatl* (*n* = 1) *Trigona* sp. (*n* = 2)	15 (8)	2011
Columnea oerstediana	Co	E	Costa Rica	Hummingbird	*Oreopyra hemileucus* (*n* = 2)	12 (6)	2010
Columnea purpusii	Cp	E	Mexico	Hummingbird	*Campylopterus hemileucurus* (*n* = 2)	8 (6)	2012
Columnea querceti[‡]	Cq	E	Costa Rica	Hummingbird	*Oreopyra hemileucus* (*n* = 7)	14 (5)	2007
Drymonia coriacea	Dc	E	Costa Rica	Hummingbird Stingless bee[§]	*Amazilia tzacatl* (*n* = 2) *Trigona* sp. (*n* = 1)	17 (8)	2011
Drymonia macrophylla	Dm	E	Costa Rica	Bee	Euglossinae (*n* = 20, 2 spp.) *Trigona* sp. (*n* = 6, 1 sp.)	12 (6)	2011, 2013
Drymonia serrulata	Ds	E	Costa Rica	Bee	*Eufriesea* sp. (*n* = 3, 1 sp.)	9 (4)	2011
Drymonia stenophylla	Dt	E	Costa Rica	Bee	*Euglossa* sp. (*n* = 3, 1 sp.)	8 (4)	2013
Kohleria spicata	Ks	R	Costa Rica	Hummingbird	*Amazilia tzacatl* (*n* = 4)	12 (12)	2011
Kohleria tigridia[‡]	Kt	E	Costa Rica	Bat	Unidentified sp. (*n* = 6)	43 (4)	2007
Monopyle maxonii[†]	Mm	T	Costa Rica	Bee	Not observed	8 (6)	2007
Paradrymonia sp.[†]	Px	E	Costa Rica	Bee	Euglossinae (*n* = 1, 1 sp.)	4 (2)	2010
Solenophora calycosa[†]	Sc	T	Costa Rica	Hummingbird	Not observed	6 (8)	2010
Insular (*n* = 28)							
Bellonia spinosa	Ba	T	Hispaniola	Bee	*Centris* sp. (*n* = 8, 2 spp.) *Trigona* sp. (*n* = 2)	18 (33)	2006, 2007
Gesneria acaulis[‡]	Ga	R	Jamaica	Hummingbird	*Anthracothorax mango* (*n* = 2)	6 (42)	2003
Gesneria calycosa[‡]	Gc	T	Jamaica	Bat	*Phyllonicteris aphylla* (*n* = 2)	7 (4)	2007
Gesneria citrina[‡]	Gi	R	Puerto Rico	Hummingbird Nectar-robbing bird[§]	*Chlorostilbon maugeus* (*n* = 13) *Coereba flaveola* (*n* = 2)	67 (90)	2003–2006
Gesneria cuneifolia[‡]	Gu	R	Puerto Rico	Hummingbird Nectar-robbing bird[§]	*Chlorostilbon maugeus* (*n* = 6) *C. flaveola* (*n* = 3)	51 (70)	2003–2006
Gesneria decapleura	Gd	R	Hispaniola	Hummingbird	*Chlorostilbon swainsonii* (*n* = 2)	10 (12)	2007
Gesneria fruticosa[‡]	Gf	T	Hispaniola	Bat	*Phyllonicteris poeyi* (*n* = 2)	21 (5)	2006–2007
Gesneria heterochroa	Gh	R	Cuba	Hummingbird Perching bird Ant[§] Cockroach[§]	*Chlorostilbon ricordii* (*n* = 5) *Setophaga caerulescens* (*n* = 8) Unidentified sp. (*n* = 5) Unidentified sp. (*n* = 4)	30 (25)	2010–2012
Gesneria humilis	Gm	R	Cuba	Moth	Unidentified sp. (*n* = 2)	31 (20)	2010–2012
Gesneria pedicellaris[‡]	Gp	R	Hispaniola	Hummingbird	*Chlorostilbon swainsonii* (*n* = 3)	14 (40)	2005–2007

(continued)

Table 1. (continued)

Species	Code	HC	Country	Pollinator/visitor functional group	Pollinator/visitor species	No. hours (plants)	Year
Gesneria pedunculosa[‡]	Ge	R	Puerto Rico	Bat	*Monophyllus redmanii* (*n* = 14)	90 (15)	2003–2007
				Perching bird[*]	*C. flaveola* (*n* = 7)		
				Fly[*]	Unidentified sp. (*n* = 5)		
				Honeybee[§]	*Apis mellifera* (*n* = 9)		
Gesneria pulverulenta[‡]	Gl	R	Hispaniola	Hummingbird	*Chlorostilbon swainsonii* (*n* = 3)	12 (6)	2006–2007
Gesneria purpurascens	Gr	R	Cuba	Hummingbird	*Chlorostilbon ricordii* (*n* = 2)	30 (20)	2010–2012
Gesneria quisqueyana[‡]	Gq	R	Hispaniola	Bat	*Monophyllus redmanii* (*n* = 4)	24 (8)	2006–2007
				Hummingbird[*]	*Chlorostilbon swainsonii* (*n* = 1)		
				Cockroach[§]	Unidentified sp. (*n* = 1)		
Gesneria reticulata[‡]	Gt	R	Puerto Rico	Hummingbird	*Chlorostilbon maugeus* (*n* = 2)	41 (40)	2004–2007
Gesneria ventricosa	Gv	T	St. Lucia	Hummingbird	*Eulampis jugularis* (*n* = 2)	7 (4)	2003
Gesneria sp. nov.	Gn	R	Hispaniola	Hummingbird	*Chlorostilbon swainsonii* (*n* = 3)	12 (32)	2007
Gesneria viridiflora subsp. *viridiflora*	Go	T	Cuba	Bat	*Monophyllus redmanii* (*n* = 5)	25 (10)	2010–2013
				Hummingbird	*Chlorostilbon ricordii* (*n* = 7)		
				Moth	Unidentified (*n* = 3, 2 spp).		
				Cockroach[§]	Unidentified sp. (*n* = 14)		
Gesneria viridiflora subsp. *sintenisii*[‡]	Gs	T	Puerto Rico	Bat	*Monophyllus redmanii* (*n* = 4)	48 (12)	2006–2007
				Hummingbird	*Chlorostilbon maugaeus* (*n* = 12)		
				Moth	Unidentified (*n* = 14, 2 spp.)		
				Ant[§]	*Solenopsis invicta* (*n* = 9)		
				Nectar-robbing bird[§]	*C. flaveola* (*n* = 1)		
Pheidonocarpa corymbosa[‡]	Pc	R	Jamaica	Hummingbird	*Trochilus* sp. (*n* = 3)	6 (6)	2004
Rhytidophyllum acunae[†]	Rc	T	Cuba	Hummingbird	Not observed	6 (14)	2012
Rhytidophyllum asperum[‡]	Ra	R	Hispaniola	Hummingbird	*Chlorostilbon swainsonii* (*n* = 14)	26 (18)	2004–2007
				Bee[*]	Halictidae (*n* = 4, 1 sp.)		
Rhytidophyllum auriculatum[‡]	Ru	T	Puerto Rico	Bat	*Monophyllus redmanii* (*n* = 4)	20 (8)	2003, 2005
				Hummingbird	*Chlorostilbon maugaeus* (*n* = 4)		
				Perching bird	*C. flaveola* (*n* = 1)		
Rhytidophyllum exsertum	Re	T	Cuba	Bat	*Monophyllus redmanii* (*n* = 8)	20 (10)	2012
				Hummingbird	*Chlorostilbon ricordii* (*n* = 5)		
				Moth	Unidentified (*n* = 3, 2 spp.)		
Rhytidophyllum grandiflorum[‡]	Rg	T	Hispaniola	Hummingbird	*Chlorostilbon swainsonii* (*n* = 4)	13 (7)	2007
				Bee	Halictidae (*n* = 6, 1 sp)		
				Fly	Syrphidae (*n* = 6, 1 sp.)		
				Moth	Unidentified (*n* = 2, 1 sp.)		
				Honeybee[§]	*Apis mellifera* (*n* = 2)		
Rhytidophyllum leucomallon[‡]	Rl	T	Hispaniola	Bat	*Monophyllus redmanii* (*n* = 9)	25 (20)	2006–2007
				Hummingbird	*Anthracothorax dominicus* (*n* = 11)		
					Chlorostilbon swainsonii (*n* = 14)		
				Moth	Unidentified (*n* = 3, 2 spp.)		
				Fly	Syrphidae (*n* = 2, 1 sp.)		
				Honeybee[§]	*Apis mellifera* (*n* = 7)		
Rhytidophyllum minus	Rm	R	Cuba	Bat	*Monophyllus redmanii* (*n* = 2)	29 (26)	2010–2013
				Hummingbird	*Chlorostilbon ricordii* (*n* = 8)		
				Moth	Unidentified (*n* = 5, 2 spp.)		
				Honeybee[§]	*Apis mellifera* (*n* = 6)		
Rhytidophyllum vernicosum[‡]	Rv	T	Hispaniola	Hummingbird	*Chlorostilbon swainsonii* (*n* = 24)	28 (14)	2006–2007
				Fly	Syrphidae (*n* = 8, 1 sp.)		
				Moth	Unidentified (*n* = 5, 1 sp.)		
				Honeybee[§]	*Apis mellifera* (*n* = 3)		

[*] Pollinator species that accounted for <20% of all visits.

[†] Pollination system inferred from the floral syndrome or from a single pollinator visit.

[‡] Pollinators reported in Martén-Rodríguez, Almarales-Castro & Fenster (2009).

[§] Non-pollinating visitors robbing nectar or pollen, visiting flowers past stigma receptivity, or introduced floral visitors.

different habitats. For simplicity, hereafter we use the term 'pollinator' to refer to all floral visitors that are potential pollinators based on contact with the reproductive organs.

We also calculated pollinator importance values considering pollinator visitation rates and contact with reproductive organs as described in Martén-Rodríguez, Almarales-Castro & Fenster (2009). We classified

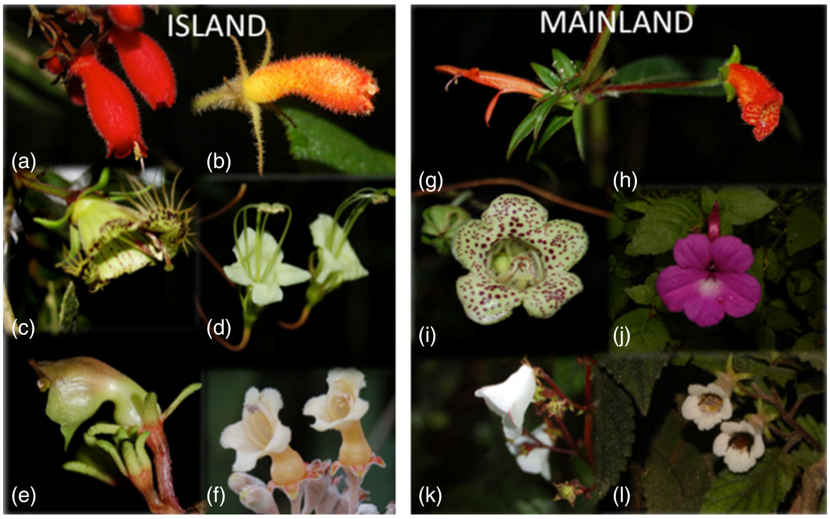

Fig. 1. A sample of Gesneriaceae species studied in the Caribbean islands (left panel) and in the mainland Costa Rica and Mexico (right panel): (a) *G. decapleura*, Hispaniola; (b) *Rhytidophyllum asperum*, Hispaniola; (c) *G. fruticosa,* Hispaniola; (d) *G. pedunculosa*, Puerto Rico; (e) *G. viridiflora*, Puerto Rico; (f) *Rhytidophyllum lanatum,* Hispaniola; (g) *G. purpusii*, Mexico; (h) *Kohleria spicata*, Costa Rica; (i) *Kohleria tigridia*, Costa Rica; (j) *Achimenes patens*, Mexico; (k) *Monopyle maxonii*, Costa Rica; (l) *Achimenes obscura*, Mexico.

pollinators into functional groups (*sensu.* Fenster *et al.* 2004; e.g. birds, bats, bees, flies) and assessed the level of functional specialization between insular and mainland environments. We considered plants as specialized when the importance index of the primary pollinator functional group was higher than 75%. The lowest index for the most important pollinator in specialized species was 84% (for bats in *G. pedunculosa*). Pollination systems were considered generalized when a given plant species had two or more functional groups of pollinators with importance values lower than 75% each (following Fenster *et al.* 2004; Martén-Rodríguez, Almarales-Castro & Fenster 2009).

SPECIALIZATION IN PLANT–POLLINATOR INTERACTIONS

To compare specialization in terms of species–species interactions between Gesneriaceae and their pollinators, we constructed quantitative pollination networks for island and mainland species separately. We used visitation rates – calculated for effective visits only (see 'Pollination systems and visitation' section) – to weight each interaction between a plant species and a pollinator species. Networks were of similar size (island = 55 species, mainland = 43 species) and strength (sum of visitation rates across the entire network: island = 9.00 visits flower^{-1} h^{-1}, mainland = 8.91 visits flower^{-1} h^{-1}). We compared species and network specialization between island and mainland Gesneriaceae using the following metrics: (i) connectance, the proportion of realized links of the total possible according to the number of plant and pollinator species (C = number of links/number of animal species × number of plant species); (ii) network specialization using the quantitative index H_2' (Blüthgen, Menzel & Blüthgen 2006), that ranges from 0 for the most generalized to 1 for the most specialized case; and (iii) plant species specialization, calculated as species degree (qualitative index, i.e. raw number of species) and as vulnerability (Bersier, Banasek-Richter & Cattin 2002), a quantitative index that takes into account the number of pollinator species and their frequency. To draw the networks and compute metrics, we used the BIPARTITE PACKAGE v. 2.04 (Dormann, Gruber & Fruend 2008; Dormann 2011) of R v. 3.1.0 (R Core Team 2014). Networks were drawn using the method cca that sorts species to produce as few crossings of interactions as possible. Species degree and effective number of partners between island and mainland species and among habitat conditions within site were compared with Kruskal–Wallis tests in R.

POTENTIAL AUTONOMOUS SELF-POLLINATION

To determine the potential for autonomous self-pollination (in the absence of pollen vectors), we tagged 7–30 individuals per plant species depending on population sizes at each study site (except for one epiphytic *Paradrymonia* species with only four individuals located at the site). We covered flower buds with bridal veil fabric bags to prevent animal visitation and assigned flowers to one of two treatments: (i) autonomous self-pollination: flowers remained covered with bags until fruiting, (ii) hand cross-pollination: virgin flowers were hand-pollinated during female phase by brushing the anthers of two different donors onto receptive stigmas. Pollen donor plants were at least 9 m away from the focal individual (following Martén-Rodríguez & Fenster 2010). We conducted treatments on flowers of the same individual for most species, and on neighbouring individuals when the species produced only one flower at a time. Fruit production was determined 6–8 weeks later, and fruit set for each species was calculated as the average proportion of mature fruits to flowers. We calculated the auto fertility index (AFI) as the ratio of bagged fruit set to outcross fruit set for each species (Lloyd & Schoen 1992).

STATISTICAL ANALYSES

Overall pollinator visitation rates and potential for autofertility between mainland and island species were evaluated using proc GLIMMIX in SAS (SAS Institute 2008). For analyses of visitation rates, the model included: the number of pollinator visits flower^{-1} h^{-1} as the response variable, and site (mainland or island), habitat condition (epiphytic, rupiculous or terrestrial), and the interaction between site and habitat condition as predictor variables. For analyses of autofertility, the same model was used but the AFI index was specified as the response variable. The models that best fit the data used a gamma distribution (with a log-link function) for analysis of visitation rates, and a binomial distribution (with a logit function) for AFI indices. Back-transformed least square means were obtained using the ilink function. We conducted two sets of analyses, one using all species in the data set and another one using hummingbird-pollinated species only. Limited sampling of species with bee, bat, lepidopteran and generalized pollination systems did not allow statistical comparisons within these functional groups. This sampling issue reflected the limited natural occurrence of particular pollination systems in either mainland or island sites. For example, the bee-pollination system was represented by seven species on the mainland and one species on the islands, whereas generalized pollination systems were represented by eight species in the islands and zero species on the mainland. For this reason, we conducted additional comparisons of visitation rates and AFI indices pooling all species and using pollination system as the predictor variable. Model distributions were as indicated above. Species with lepidopteran pollination were excluded from these analyses because they had only one species representative of each pollination system (butterfly and moth).

We also conducted nonparametric correlation analyses between visitation rates and AFI indices, and visitation rates and plant species degree (equivalent to number of pollinator species). These analyses were conducted for the overall set of species, and for insular and mainland species separately. For the insular data set, we conducted two sets of analyses to include the phylogenetic information available (Martén-Rodríguez *et al.* 2010). Phylogenetic independent contrasts (PICs) were calculated to test for the association between pollinator visitation rates and plant species degree and between visitation rates and AFI indices using the PADP module in MESQUITE version 2.75 (Maddison & Maddison 2011). For the mainland data set, only a few study species were previously included in published phylogenies of the family Gesneriaceae; therefore, phylogenetically informed analyses were not possible on this data set.

Results

POLLINATION SYSTEMS, SPECIALIZATION AND VISITATION RATES

The pollinators of the study species included bats, bees, butterflies, flies, hummingbirds and moths, but not all pollination systems were equally represented in mainland and insular sites (Table 1, Fig. 2). The low number of individual pollinators observed for various species was the result of low visitation rates to flowers of most Gesneriaceae species. Hummingbird pollination was the most common system in both regions, and specialized pollination by moths was rare in

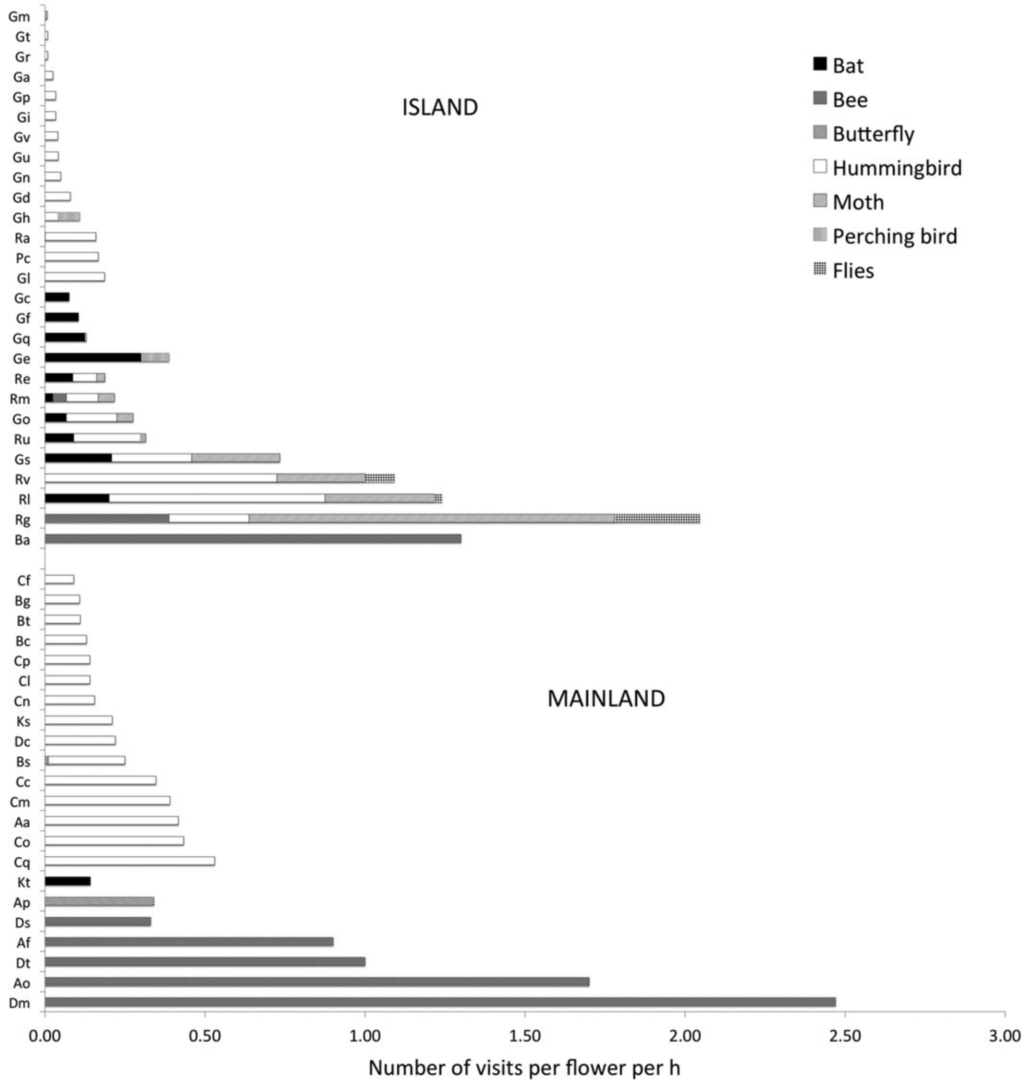

Fig. 2. Pollinator visitation rates for 22 species of Gesneriaceae from mainland Costa Rica and Mexico and 27 species of Gesneriaceae from the Caribbean islands. Species codes shown on vertical axis correspond to species as listed in Table 1.

both regions. Bee pollination was more frequent on the mainland, and bat pollination was more frequent on the islands. Butterfly pollination was rare and only recorded in mainland sites. In the mainland, all species were functionally specialized, that is, more than 90% of the visits to flowers of each plant species were made by one functional group of pollinators (Fig. 2). On the islands, 71% of the species were functionally specialized and the remaining species had mixed pollination systems that included bats, birds and insects (Fig. 2).

Floral visitors that were not considered potential pollinators were recorded in three mainland and 11 insular Gesneriaceae species (Table 1). These visitors included small bees that approached flowers to collect pollen from anthers or to take nectar without making contact with the reproductive organs of the flower; most of these visitors were observed in species with bell-shaped corollas). There were also visits by nectar-robbing birds (*Coereba flaveola*), which extracted nectar by poking a whole at the base of the corolla (only on the islands). Interestingly, these birds were also considered effective pollinators of two insular species, where they fed by inserting their heads into the flower contacting both male and female reproductive organs (Table 1). Finally, there were infrequent visits by cockroaches and ants that entered bell-shaped flowers apparently looking for nectar without contacting stigmas or anthers.

Both island and mainland Gesneriaceae pollination networks (Fig. 3) were specialized with low connectance (island = 0.064, mainland = 0.055) and high H_2' specialization (island = 0.73, mainland = 1.00). Overall, Gesneriaceae species had a small number of pollinator species. Mainland plant species had a lower number of pollinator species than insular plant species (degree: $\chi^2 = 5.63$, d.f. = 1, $P = 0.018$, range: 1–3 pollinators for mainland species, 1–6 pollinators for insular species; effective partners: $\chi^2 = 5.49$, d.f. = 1, $P = 0.019$ range: 1–2.6 for mainland, 1–4.4 for insular species; $n = 49$; Fig. 3). Species with generalized pollination systems had the highest number of pollinator species (Fig. 3). The number of pollinator species per plant did not differ among habitat conditions on the mainland (degree: $\chi^2 = 0.18$, d.f. = 2, $P = 0.913$; effective partners: $\chi^2 = 0.22$, d.f. = 2, $P = 0.895$; $n = 22$), but insular terrestrial species had a higher number of pollinators than insular rupiculous species (degree: $\chi^2 = 7.59$, d.f. = 1, $P = 0.006$, range 1–6 pollinators for terrestrial, and 1–4 pollinators for rupiculous species; effective partners: $\chi^2 = 8.40$, d.f. = 1, $P = 0.004$, range 1–4.4 pollinators for terrestrial and 1–2.7 pollinator for rupiculous species; $n = 27$).

Pollinator visitation rates (mean visits flower^{-1} h^{-1}) differed among species with different pollination systems ($F_{(3,43)} = 14.76$, $P < 0.0001$; Table 2). Visitation rates were highest for bee-pollinated Gesneriaceae and lowest for moth-pollinated species. Overall visits flower^{-1} h^{-1} ranged between 0.01 and 2.05 visits in the islands, and between 0.1–2.47 visits in the mainland. Mean visitation rates did not differ between island and mainland species ($F_{(1,44)} = 0.68$, $P = 0.414$; Fig. 4a), nor between habitat conditions ($F_{(2,44)} = 1.89$, $P = 0.164$; Fig. 4a). There was a significant interaction between habitat condition and site ($F_{(1,44)} = 15.39$, $P = 0.0003$), indicating low visitation on islands and high visitation on the mainland for rupiculous species only (Fig. 4a). Visitation rates were not correlated with the number of pollinator species for the set of mainland species ($r = 0.283$, $P = 0.203$, $n = 22$), but the two variables were positively correlated for the set of insular species ($r = 0.807$, $P < 0.001$, $n = 27$). The latter correlation was also significant in the PIC analysis of insular species ($r = 0.619$, $P = 0.005$, $n = 18$ contrasts).

For the set of hummingbird-pollinated species, pollinator visits flower^{-1} h^{-1} ranged between 0.01 and 0.21 on islands and between 0.10 and 0.53 on the mainland. Mean visitation rates were on average, three times higher in the mainland (0.24 ± 0.035 visits flower^{-1} h^{-1}) than in the islands (0.07 ± 0.07 visits flower^{-1} h^{-1}) ($F_{(1,23)} = 6.11$, $P = 0.021$; Fig. 4b), but there were no significant differences among habitat conditions ($F_{(2,23)} = 0.12$, $P = 0.893$; Fig. 4b), and no interaction between site and habitat condition ($F_{(1,23)} = 0.78$, $P = 0.388$, Fig. 4b).

POTENTIAL AUTONOMOUS SELF-POLLINATION

The potential for autonomous self-pollination was highly variable among species, with AFI indices ranging between 0 and 1 in both environments. AFI values for all study species are listed in Table 3. In the comparison of pollination systems, AFI indices were highest for species with moth pollination and lowest for species with bat pollination ($F_{(3,40)} = 9.66$, $P < 0.0001$; Table 3).

There were no significant differences in mean AFI indices between island and mainland for the complete set of species ($F_{(1,42)} = 0.11$, $P = 0.742$; Fig. 4c). However, there was a trend for rupiculous and epiphytic species to have higher autofertility than terrestrial species (Fig. 4c, $F_{(2,42)} = 3.16$, $P = 0.053$). The interaction between site and habitat condition was not significant ($F_{(1,42)} = 0.11$, $P = 0.741$; Fig. 4c). For hummingbird-pollinated species, there were no significant differences between sites ($F_{(1,22)} = 0.01$, $P = 0.940$; Fig. 4d), habitat conditions ($F_{(2,22)} = 1.14$, $P = 0.338$; Fig. 4d) and no interaction between site and habitat condition ($F_{(1,22)} = 0.12$, $P = 0.731$; Fig. 4d).

There were no significant correlations between pollinator visitation rate and the AFI index for the overall set of species ($r = -0.12$, $P = 0.442$, $n = 42$), nor for the set of mainland species ($r = 0.333$, $P = 0.164$, $n = 19$), but there was a significantly negative correlation between these two variables for insular species ($r = -0.537$, $P = 0.008$, $n = 23$). However, in the PIC analysis for insular species, the latter association was not significant ($r = -0.146$, $P = 0.551$, $n = 18$ contrasts).

Discussion

Insular ecosystems generally have a lower diversity and abundance of plant and animal species than mainland

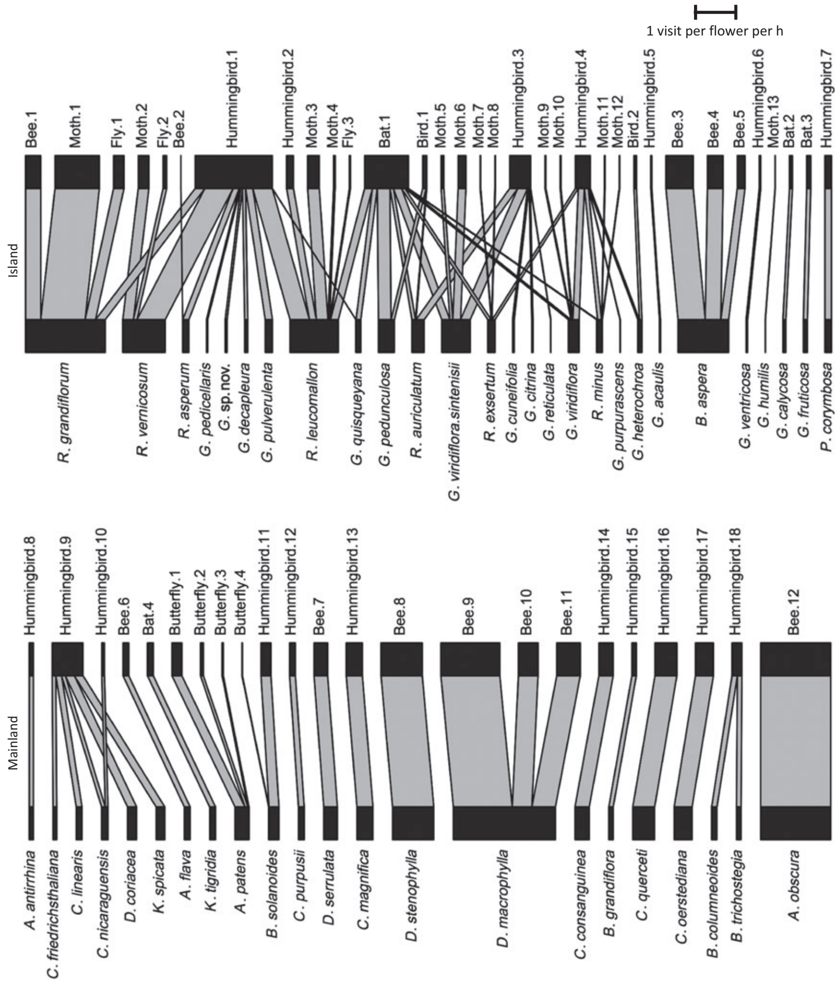

Fig. 3. Pollination networks for island (top) and mainland (bottom) species of Gesneriaceae and their pollinators. On each network, top rectangles represent pollinator species, and bottom rectangles represent plant species. Links between species are weighted by visitation rates; thus, rectangle widths are proportional to a species total visitation rate.

ecosystems (MacArthur & Wilson 1967; Inoue 1993). This study tested the hypothesis that pollinator-depauperate insular faunas would be associated with low pollinator visitation, which in turn would have selected for lower pollination specialization and greater rates of autonomous self-pollination in insular than in mainland plant species. Alternatively, low species diversity could lead to a reduced number of biotic interactions on islands, resulting in frequent pollination specialization in these environments. Studies of plant-pollination networks comparing insular and mainland communities at a global scale support the view that specialization increases in insular environments (Olesen & Jordano 2002; Trojelsgaard & Olesen 2013). This study revealed a high degree of functional specialization both in insular and mainland Gesneriaceae; however, generalized pollination systems were only recorded in species from the Caribbean islands. Pollinator visitation rates were lower in island than in mainland sites for hummingbird-pollinated species only, and there were no differences in the rates of self-pollination between insular and mainland species. Below we discuss possible causes and evolutionary implications of the observed trends in pollinator visitation, specialization and autofertility between island and mainland environments.

POLLINATOR AVAILABILITY AND SPECIALIZATION

The difference in the level of functional specialization between island and mainland relatives documented in this study was not related to differences in the overall frequency of pollinator visitation between sites. Studies comparing pollinator visitation between insular and mainland plant populations generally report lower visitation on islands (e.g. Inoue, Maki & Masuda 1996), but no differences between environments have also been reported (e.g. Schueller 2004). In Caribbean Gesneriaceae, overall pollinator visitation patterns differed from visitation rates to ornithophilous species, which were on average, three times greater in mainland than in insular sites. Thus, considering that hummingbird pollination is the ancestral state for the Antillean clade (Martén-Rodríguez *et al.* 2010), transitions to bat and mixed pollination systems are consistent with an adaptive response to cope with a putatively low and variable pollinator visitation experienced by the early colonizers of the islands. This idea is supported by an earlier study that showed that the reproductive success of Caribbean Gesneriaceae was limited by pollen only in hummingbird-pollinated species (Martén-Rodríguez & Fenster 2010).

A lower level of specialization in plant–animal interactions on islands would also be expected if feeding niches

Table 2. Pollinator visitation rates (mean visits flower^{-1} h^{-1}) and autofertility (AFI) indices for Gesneriaceae species studied in island and mainland environments in the Caribbean basin during 2004–2013. The autofertility index (Lloyd & Schoen 1992) was calculated as the fruit set of bagged flowers divided by the fruit set of outcrossed flowers. Sample size indicates the number of species observed or sampled for each pollination system. Different superscript letters indicate values statistically different after Tukey comparisons. Butterfly and moth pollination systems were not included in the analyses due to low sample sizes

Species	Visitation rate ± SE	*n*	AFI ± SE	*n*
Bat	0.17 ± 0.065^{A}	5	0.01 ± 0.050^{a}	4
Bee	1.16 ± 0.395^{B}	6	0.59 ± 0.220^{b}	5
Butterfly	0.34	1	0.11	1
Generalized	0.75 ± 0.231^{B}	8	0.10 ± 0.104^{a}	8
Hummingbird	0.15 ± 0.025^{A}	28	0.34 ± 0.091^{ab}	27
Moth	0.01	1	0.82 ± 0.175	2

expanded due to increased ecological opportunity and competitive release on insular environments (Yoder *et al.* 2010). The approach used in this study did not allow an assessment of all floral resources used by pollinators of Caribbean Gesneriaceae, but results suggest that broad feeding niches may be common in hummingbirds and bats on the Caribbean islands. For example, the hummingbird *Chlorostilbon swainsonii* (hummingbird 1 on Fig. 3) visits most species with generalist and ornithophilous flowers on Hispaniola (Fig. 3), as well as other plant species not formally documented in this study (S. Martén-Rodríguez, pers. obs.). Likewise, results from a study of plant–hummingbird interactions on Trinidad and Tobago showed a broader use of floral resources by hummingbirds on the smaller and more remote island of Tobago (Feinsinger, Wolfe & Swarm 1982). From the plant's perspective, a broader use of pollinator niche space was also observed in this study. On the Caribbean islands, 29% of Gesneriaceae species exhibited mixed

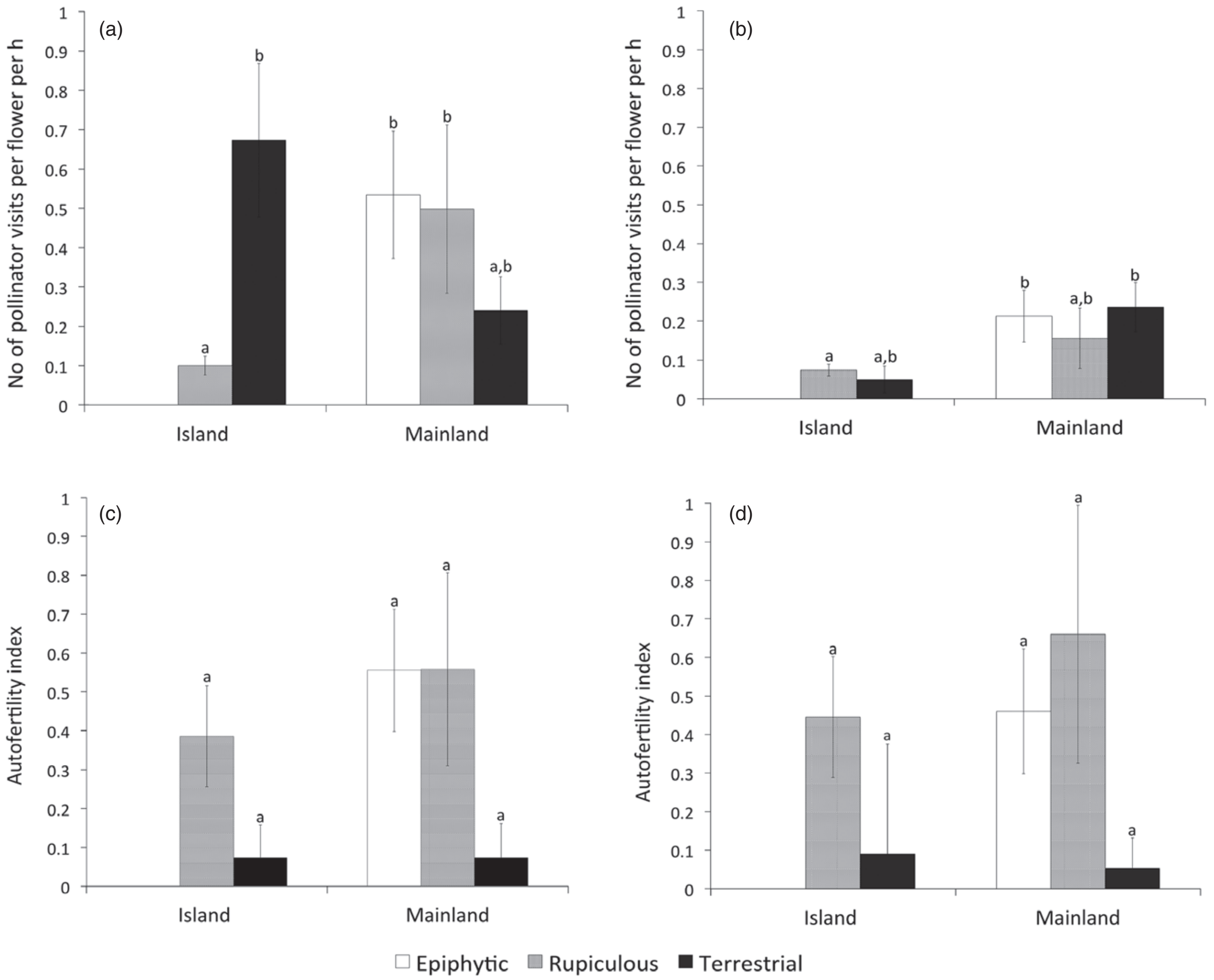

Fig. 4. Back-transformed means (± SEM) of pollinator visitation and the autofertility index for island and mainland species of Caribbean Gesneriaceae. Pollinator visitation is considered as the number of visits flower^{-1} h^{-1} for the complete set of species (a) and for hummingbird-pollinated species (b). The AFI index was calculated as the fruit set of bagged flowers divided by the fruit set of outcrossed flowers (Lloyd & Schoen 1992) for the complete set of species (c) and for hummingbird-pollinated species (d). Superscript letters indicate significant differences between treatments after Tukey HSD at $P < 0.05$.

Table 3. Mean fruit set of bagged flowers, outcrossed flowers and autofertility index for 47 species of Gesneriaceae studied in Costa Rica, México and the Caribbean islands in 2006–2013. The autofertility index (Lloyd & Schoen 1992) was calculated as the fruit set of bagged flowers divided by the fruit set of outcrossed flowers

Species	Pollination system	Autonomous fruit set	Outcross fruit set	AFI index	*n*
Mainland (*n* = 23)					
A. flava	Bee	0.28	0.35	0.80	14
D. macrophylla	Bee	0.45	0.56	0.80	7
M. maxonii	Bee*	0.10	0.33	0.24	7
Paradrymonia sp.	Bee*	0.74	0.75	0.99	4
K. tigridia	Bat	0.00	0.58	0.00	8
A. patens	Butterfly	0.08	0.72	0.11	13
A. antirrhina	Hummingbird	0.21	0.32	0.66	17
B. columneoides	Hummingbird	0.01	0.50	0.02	15
B. grandiflora	Hummingbird	0.00	0.38	0.00	9
B. solanoides	Hummingbird	0.00	0.87	0.00	16
B. trichostegia	Hummingbird	0.00	0.74	0.00	11
C. friedrichsthaliana	Hummingbird	0.00	0.50	0.00	12
C. consanguinea	Hummingbird	0.69	0.83	0.83	7
C. linearis	Hummingbird	0.23	0.43	0.53	13
C. magnifica	Hummingbird	0.21	0.77	0.34	10
C. nicaraguensis	Hummingbird	0.00	0.89	0.00	18
C. oerstediana	Hummingbird	0.15	0.79	0.19	13
C. purpusii	Hummingbird	0.25	0.62	0.4	8
C. querceti	Hummingbird	0.17	0.81	0.21	15
D. coriacea	Hummingbird	0.39	0.59	0.66	10
K. spicata	Hummingbird	0.45	0.68	0.66	14
S. calycosa	Hummingbird*	0.00	0.86	0.00	7
C. crassifolia	Moth*	0.51	0.50	1.02	7
Island (*n* = 24)					
B. aspera	Bee	0.09	0.64	0.14	21
G. citrina[†]	Hummingbird	0.24	0.63	0.38	30
G. cuneifolia[†]	Hummingbird	0.68	0.77	0.88	15
G. decapleura	Hummingbird	0.00	0.72	0.00	10
G. heterochroa	Bird	0.08	0.89	0.09	12
G. pedicellaris	Hummingbird	0.87	0.79	1.10	12
G. pulverulenta[†]	Hummingbird	0.13	0.68	0.19	8
G. purpurascens	Hummingbird	0.69	1.00	0.69	16
G. reticulata[†]	Hummingbird	0.90	0.92	0.98	28
G. sp. nov.[†]	Hummingbird	0.04	0.57	0.07	21
R. acunae	Hummingbird*	0.08	0.89	0.09	14
R. asperum[†]	Hummingbird	0.12	0.71	0.17	23
G. humilis	Moth	0.65	1.00	0.65	12
G. fruticosa[†]	Bat	0.00	0.31	0.00	10
G. pedunculosa[†]	Bat	0.01	0.50	0.02	22
G. quisqueyana[†]	Bat	0.01	0.53	0.02	21
G. viridiflora subsp. *viridiflora*	Generalist	0.08	1.00	0.08	16
G. viridiflora subsp. *sintenisii*[†]	Generalist	0.08	0.89	0.09	15
R. auriculatum[†]	Generalist	0.04	0.64	0.06	19
R. exertum	Generalist	0.18	1.00	0.18	12
R. grandiflorum	Generalist	0.04	1.00	0.04	21
R. leucomallon[†]	Generalist	0.03	1.00	0.03	19
R. minus	Generalist	0.20	0.77	0.26	22
R. vernicosum[†]	Generalist	0.02	0.67	0.03	30

*Pollination system inferred from the floral syndrome.

[†] Autonomous self-pollination reported in Martén-Rodríguez & Fenster (2010).

pollination systems, while on the mainland, all study species were highly specialized, both functionally (one pollinator functional group) and ecologically (1–3 pollinator species). This is also the case of other groups of mainland Gesneriaceae in the Neotropics, where 1–3 pollinator species per plant species have been reported (e.g. SanMartin-Gajardo & Sazima 2004, 2005; Carlson 2007). Interestingly, there was an asymmetry in plant–pollinator interactions in insular environments, with highly specialized plant species receiving visits by pollinators that use a broad range of Gesneriaceae species (Fig. 3).

The high frequency of specialized Gesneriaceae species on the Caribbean islands is notable, since studies of plant–pollinator networks in the Lesser Antilles have shown a low degree of functional specialization in hummingbird-pollinated communities, particularly associated with hummingbird size and elevation (Dalsgaard *et al.* 2008, 2009). In these Lesser Antillean communities, plant species visited by large hummingbirds and species occurring at higher elevations tend to be functionally specialized, while plant species visited by small hummingbirds and species occurring at lower elevations tend to be pollinated by hummingbirds and insects (Dalsgaard *et al.* 2009). Most ornithophilous species of Antillean Gesneriaceae occur between 300 and 1500 m in mountainous wet regions, and they are predominantly visited by short-billed hummingbirds*;* few of these plant species are also visited by insects (Table 1). Altitudinal variation in insect abundance does not explain the high specialization in ornithophilous Gesneriaceae, since insect visitation to flowers exhibiting other pollination syndromes occurred at all elevations. Therefore, high pollination specialization may instead be related to floral traits that restrict insect entrance or extraction of rewards (e.g. tubular corollas, constrictions above nectar chamber and inserted reproductive organs).

Specialized hummingbird pollination, where plant species are pollinated exclusively by one or few bird species, is common in both tropical and temperate communities, particularly in studies conducted at one or few sites (e.g. Feinsinger 1976; Brown & Kodric-Brown 1979; Rodrigues & Rodrigues 2014). However, the level of ecological specialization of any given plant species is likely to decrease at broader geographic scales due to spatial variation in pollinator faunas (e.g. Dalsgaard *et al.* 2009). Plant species included in this study were observed at a single site; therefore, it is possible that pollination systems are less ecologically specialized across the species geographic ranges. On the pollinator's side, extreme specialization is not expected because most plant species have flowering seasons restricted to weeks or months of the year, while animals, such as hummingbirds and bats, have to feed all year round. Nonetheless, at particular communities and times of the year specialized pairwise interactions between plants and pollinators may occur (e.g. Temeles & Kress 2003).

Specialized visitation by one or few hummingbird species to particular plant species are possible if bird species preferentially feed on a limited set of the floral resources available at a given time in a community. Resource partitioning by birds may be related to interference competition between hummingbirds (Feinsinger & Colwell 1978), or to differences in plant traits (e.g. floral morphology, energy rewards, plant phenology and spatial distribution), and hummingbird characteristics (e.g. bird behaviour, bill size and shape, body size and energy requirements; Stiles 1975; Feinsinger 1976; Kodric-Brown *et al.* 1984; Temeles & Kress 2003). Thus, ornithophilous plants may specialize on different functional groups of hummingbirds with different morphological traits and behaviours (e.g. long-billed vs. short-billed, Kodric-Brown *et al.* 1984; territorial vs. traplining, Stiles 1975). Furthermore, specialization may occur in plant species with multiple floral visitors due to differences in pollination efficiency among visitor species. For example, a recent study showed that the understorey tropical herb *Heliconia tortuosa* was visited by six different hummingbird species; however, only hummingbirds with long-curved bills significantly contributed to pollination success (Betts, Hadley & Kress 2015).

FREQUENCY OF POLLINATION SYSTEMS

This study showed that hummingbird pollination was equally common in insular and mainland sites, but the frequencies of other pollination systems differed between the two regions. For example, bee pollination was rare in the insular Gesneriaceae possibly reflecting low diversity and abundance of this insect group in the Caribbean islands (Supporting information 2). Other insects were uncommon in both environments, although moths were relatively frequent floral visitors of plant species with mixed pollination systems on the islands (Fig. 2). Likewise, bat pollination was more common on the islands, despite the fact that bats are more diverse on the mainland. It has been estimated that flowers pollinated by bats evolved at least five times in the insular clade Gesneriinae (encompassing specialized bat- and mixed pollination systems) (Martén-Rodríguez *et al.* 2010). Since bats are known for their capacity to transfer large pollen loads over long-distances (Bawa 1990; Quesada *et al.* 2004), selection for outcrossing may also underlie evolutionary transitions to bat pollination in insular Caribbean Gesneriaceae (Martén-Rodríguez *et al.* 2010). Accordingly, this study showed that across all pollination systems, species pollinated by bats – including bat specialists and generalists – had the lowest potential to self-pollinate (Table 2).

AUTOFERTILITY ON ISLAND AND MAINLAND ENVIRONMENTS

It has been proposed that outcrossing breeding systems may be favoured after island establishment to reduce the deleterious consequences of inbreeding (Barrett, Emerson & Mallet 1996; Sakai *et al.* 2006). However, the high occurrence of autogamous breeding systems on islands is possibly explained by the reproductive assurance advantage conferred by self-pollination during island colonization and establishment if pollinators are rare (Baker 1955, Barrett, Emerson & Mallet 1996). In this study, insularity was not associated with high autofertility, which may reflect genetic processes acting against self-fertilization after island colonization, such as small effective population sizes, frequent founder events and low levels of genetic diversity (Barrett, Emerson & Mallet 1996; Frankham 1997; Hufford, Mazer & Hodges 2014). These factors may lead to high levels of inbreeding depression in island plants (Sakai *et al.* 1997; Culley *et al.* 1999). In Caribbean Gesneriaceae, the broad scope of autofertility levels (from 0 to 1) suggests that selection against selfing breeding systems is acting strongly only in some species, with most species apparently maintaining mixed breeding systems (Table 3).

Other factors may also influence the frequency of autofertility both in island and mainland Gesneriaceae. In particular, this study revealed that potential autonomous self- pollination was higher in rupiculous and epiphytic than in terrestrial species in both environments. The predominance of self-compatible species in epiphytic plant groups from tropical montane habitats has been related to the unpredictable and unfavourable weather conditions for pollination in these environments (Bawa 1990; Bush & Beach 1995; Tremblay *et al.* 2005). However, in Caribbean Gesneriaceae, pollinator visitation rates were only low for rupiculous species on islands; therefore, low pollinator visitation by itself does not account for the generally higher autofertility exhibited by rupiculous and epiphytic species across regions. Since rocky and epiphytic habitats generally exhibit limited or temporally variable water and resource availability (Benzing 1990; Pereira-Dias & Santos 2015), we hypothesize that selection may favour the evolution of autonomous breeding systems in these habitats to maximize the use of the resources assigned to reproduction in unpredictable pollinator environments. In addition, a recent meta-analysis showed that long-lived shrubs and trees generally experience greater inbreeding depression than herbaceous plants (Angeloni, Ouborg & Leimu 2011); therefore, it is possible that terrestrial Gesneriaceae species, mostly represented by shrubs and small trees, experience greater selection against floral traits that facilitate self-fertilization.

PHYLOGENETIC CONSIDERATIONS

Patterns of pollinator and breeding system evolution in insular and mainland relatives could be partly explained by phylogeny, particularly if evolutionary relationships were closer between species located within each region. While a phylogeny that includes all mainland study species is currently unavailable, existing phylogenetic information indicates that mainland species belong to various subtribes within the tribes Gesnerieae and Beslerieae (Weber, Clark & Möller 2013). These clades exhibit great variation in floral phenotypes suggesting various independent origins of different pollination systems (Roalson, Skog & Zimmer 2003; Roalson *et al.* 2005). The Antillean study species belong to a single clade (subtribe Gesneriinae within Tribe Gesnerieae), which would make insular species phylogenetically less independent than mainland species. However, insular Gesneriinae encompass several independent origins of different pollination and breeding systems (Martén-Rodríguez *et al.* 2010). Furthermore, no overall differences in pollinator visitation and autofertility were found between insular and mainland species. Consequently, the documented variation in these variables among sites is, according to the available evidence, largely independent of phylogeny.

Conclusions

Overall, this study found that patterns of pollinator visitation and reproductive assurance between mainland and island relatives are more complex than expected. In general, there is high specialization in pollination systems in both environments, although insular species have a greater frequency of mixed pollination systems. Hummingbird visitation is lower on islands, supporting the idea that pollen limitation drives transitions from hummingbird pollination to other pollination and breeding systems. In contrast, generalized pollination is associated with higher pollinator visitation, which possibly translates into greater reproductive success in the absence of other reproductive assurance mechanisms. Autofertility rates vary greatly among species in both island and mainland regions, possibly reflecting intricate interactions between pollinator visitation, plant breeding systems and the environment. The widespread occurrence of autonomous self-pollination in insular and mainland environments suggests the advantages of this breeding system are context dependent and should be evaluated across different plant lineages and environments.

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Data accessibility

Study locations for each species are uploaded as online supporting information. Species richness of pollen and nectar-feeding animal species at study countries uploaded as online supporting information. Pollinator visitation data are uploaded as online supporting information. Autofertility data are included in the article (Table 3).

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Geographic location of 54 Gesneriaceae species studied in Costa Rica, Mexico, Cuba and Dominican Republic between 2004 and 2014.

Appendix S2. The number of species in animal taxonomic groups that contain primarily nectar- or pollen-feeding species in the mainland and island study sites.

Appendix S3. Pollinator visitation rates by pollinator functional group for Gesneriaceae species studied in insular and mainland Caribbean locations between 2004 and 2014.

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