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Pollination-related functions of decorative sterile flowers of nine Japanese *Hydrangea* species (Hydrangeaceae)

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Abstract

Most species of *Hydrangea* (Hydrangeaceae) have a flower arrangement in which several large sterile decorative flowers surround a dense cluster of small fertile flowers. These decorative flowers have been hypothesized to attract pollinators, but this has yet to be tested for this genus. To identify whether the decorative flowers have functions related to pollination success, we carried out field manipulation experiments in which we clipped or mounted decorative flowers of nine *Hydrangea* species, eight with and one without inherent decorative flowers, and recorded insect visits to the intact and treated inflorescences. Results showed that for most of the studied species the presence of decorative flowers increased the frequency of visits and weakly increased the frequency of visits per unit area to inflorescences. Decorative flowers appeared to act as landing-sites for three species for which flowers represented a high proportion of the inflorescence-surface area (i.e. *H. scandens*, *H. luteovenosa*, *H. macrophylla*). The results suggest that the main function of decorative flowers of the studied *Hydrangea* species is to boost attractiveness to pollinators by increasing the inflorescence-surface area, whereas the landing-site function was evident only in certain species.

framed inflorescence; *Hydrangea*; flower dimorphism; sterile flower; visual attraction; landing-site function

Introduction

In zoophilous flowering plants, the spatial and temporal aspects of floral arrangement can affect the attractiveness of inflorescences to pollinators. The number of inflorescences and their individual attractiveness (related to the presence of ray flowers) interact to affect fruit set, as suggested by the study by Andersson (1996) for *Jacobaea vulgaris* Gaertn (Asteraceae). Among flowering plants, sterile flowers, which do not produce reproductive structures or pollen, such as ray flowers, are found in several families and might play a role in pollination success. Inflorescences with both sterile and fertile flowers are found in some distantly-related plant families: Asparagaceae (Morales et al. 2013), Orchidaceae (Meisel et al. 2014), Adoxaceae, Hydrangeaceae (Darwin 1877), Apiaceae, Lamiaceae, and Asteraceae (Plitmann 1995). Although the functions of sterile flowers have been generally under-investigated, the efficacy of this mechanism has been established to some extent. The presence of sterile flowers has been documented to increase fruit and seed set (Bell 1985; Andersson 1991; Andersson 2008; Jin et al. 2010), number of pollen grains on stigmas (Jin et al. 2010), and pollinator visitation rates (Andersson 1991; Celedón-Neghme et al. 2007; Jin et al. 2010; Morales et al. 2013).

The inflorescences of most species of *Hydrangea* (Hydrangeaceae) are composed of a dense cluster of numerous small hermaphrodite flowers, surrounded by some large, showy, sterile flowers (from now on referred as to 'decorative flowers'). This floral arrangement is referred to as 'framed inflorescences' and is also seen in *Viburnum* (Adoxaceae). Darwin (1877) speculated that the decorative flowers of framed inflorescences of *Hydrangea* and *Viburnum* might increase their attractiveness to pollinators. The pollinator-attracting function of such flowers has also been postulated by other authors (Donoghue 1980; Pilatowski 1981; Jacobs 2010), but the hypothesis has only been tested for a few *Viburnum* species. Bell (1985) and Jin et al. (2010) showed that the presence of decorative flowers in *Viburnum* spp. increased pollination success and/or pollinator visitation. On the other hand, Krannitz and Maun (1991) did not observe any significant change in fruit set for *V. opulus* L. when decorative flowers were removed. As most species of *Hydrangea* have framed inflorescences similar to *Viburnum*, decorative flowers of *Hydrangea* spp. may also increase

the frequency of visits by pollinators. Decorative flowers might also have a landing-site function, which has never been tested before in species with framed inflorescences. We base this assumption on the impression that it is easier for insect pollinators to land on decorative flowers because they are more conspicuous, are located in the border of the inflorescence and represent a considerable proportion of the inflorescence-surface area.

In Hydrangeaceae, 5 of 16 genera have species that display both sterile and fertile flowers within a single inflorescence: *Cardiandra*, *Deinanthe*, *Hydrangea*, *Platycrater*, and *Schizophragma* (Hufford 1997; Jacobs 2010). Among those genera, only *Cardiandra*, *Hydrangea*, and *Schizophragma* contain species with framed inflorescences. Most *Hydrangea* species possess framed inflorescences (FR species), and only four species do not (n-FR species) (Hufford 1997; Jacobs 2010). The question that arises from the presence of framed inflorescences in *Hydrangea* is: Does the presence of decorative flowers enhance pollinator visitation in FR species of *Hydrangea*?

To address the question, we examine whether the presence of decorative flowers is related to pollination success. In particular, we test the hypothesis that decorative flowers increase the frequency of pollinator visits and serve as landing-sites for pollinators. We conducted field experiments in which decorative flowers were clipped on FR species and mounted on n-FR species. We investigated insect fauna visiting framed and non-framed inflorescences. Next, we compared the visitation frequencies and types of insect flower visitors to framed and non-framed inflorescences (i.e. intact and treated inflorescences) among nine Japanese *Hydrangea* species comprising 8 FR and 1 n-FR species. We expected decorative flowers to increase the frequency of pollinators visits and function as landing-sites for insect visitors. Based on the data, we discuss the function, evolution and diversification of such flowers in *Hydrangea*.

Material and methods

Study sites and species

Hydrangea species occur mainly in temperate regions of eastern Asia and North America, and extends southward into the tropics (McClintock 1957; Zhaofen and Bartholomew 2001). The Japanese archipelago is characterized by high *Hydrangea* diversity (McClintock 1957), with 14 species (Hinkley 2003; Kawarada et al. 2010), most of which are shrubs. Most species of this genus display framed inflorescences: large, sterile, decorative flowers surrounding a cluster of numerous, small, fertile flowers. It is common among cultivar variations that decorative flowers replace the fertile flowers. The fertile flowers are bisexual, have short pedicels, and are much more numerous than the decorative flowers. The decorative flowers of *Hydrangea* are usually sterile, although there are some rare cases of fertile decorative flowers in *H. macrophylla* (Uemachi et al. 2004).

We observed and recorded insect visits to flowers of the following nine *Hydrangea* species: *H. hirta* (Thunberg) Siebold., *H. involucrata* Siebold., *H. luteovenosa* Koidz., *H. scandens* Seringe., *H. serrata* (Thunberg) Seringe., *H. sikokiana* Maxim., *H. paniculata* Sieb. and Zucc., *H. petiolaris* Sieb. and Zucc., and *H. macrophylla* (Thunb.) Ser. Among the nine species, eight were FR species, and *H. hirta* was a n-FR species (Table 1, Fig. 1). The observations and recordings were conducted in seven distinct locations on the Honshu island, Japan between 2014 and 2015 (supplementary Table S1). The decorative flowers had enlarged showy sepals surrounding a cluster of small fertile flowers forming a 'frame' (Fig. 1), but there were too few decorative flowers to form a complete frame in *H. scandens* and *H. luteovenosa* (Fig. 1F, G). The decorative flowers of most species point upwards, but those of *H. involucrata* are directed laterally (Fig. 1A). The decorative flowers of *H. sikokiana* are small in size and proportion in contrast to the cluster of fertile flowers and to the corresponding decorative flower of the other studied species, their sepal area occupies less than 10% of the area of the whole inflorescence (Table 1, Fig. 1E). The inflorescences are all corymbs except in the case *H. paniculata*, whose inflorescence is a panicle (Table 1, Fig. 1H).

Observation of flower visitors

We recorded insect visits to six pairs of inflorescences for each *Hydrangea* species, each pair with one framed and one non-framed inflorescence. These pairs had inflorescences of similar forms (e.g., size and number of decorative flowers), and were selected from the same plant when possible. If one individual plant did not have enough inflorescences, we used individuals close by. Within the inflorescence pair, one inflorescence was kept intact, and the other was treated (i.e. decorative flowers were clipped in FR species and mounted in n-FR species); for *H. hirta*, purple decorative flowers of an *H. macrophylla* cultivar were mounted. We recorded insect visits with video cameras (Panasonic HC-V210M, Panasonic HC-V520M and Panasonic HC-V620M) over the course of about 4 hours for each inflorescence pair.

We analysed recorded flower visits to obtain data on the frequency of visitations and landing-site (decorative or fertile flowers) for each flower visitor species. Additionally, in order to assess nectar production, we measured the volume of floral nectar in bagged inflorescences with glass micropipettes (0.5 μ l), and the sugar concentration of the nectar with sugar refractometers (KIKUCHI, Tokyo, Japan).

Statistical analysis

We evaluated the hypothesized functions of decorative flowers by analysing data obtained from recorded flower visits with three pairs of generalized linear models (GLM) with R version 3.5.0 (R Core Team 2018). The first GLM of each pair assessed associations broadly for all studied species, whereas the second GLM assessed the associations individually for each studied species.

To identify whether decorative flowers increase the frequency of pollinator visits, we applied two GLM pairs with Gamma distribution (R package: stats; function: glm; R Core Team 2018). The first GLM pair was used to identify the association between framing (presence of decorative flowers) and the frequency of pollinator visits. The response variable was the visitation rate (visits/inflorescence/h) for both GLM. The predictor variables were the framing and the interaction

between species and framing for the first and the second GLMs, respectively. For the latter GLM, the framing was the factor chosen as the intercept (baseline reference in the regression).

The second GLM pair was used to identify the association between the inflorescence-surface area (cluster of fertile flowers and decorative flowers, or only the cluster of fertile flowers, according to the treatment of sample and framing of species) and the frequency of pollinator visits per unit area. The response variable was the adjusted visitation rate (visits/inflorescence/h/cm²). The predictor variables were the framing and the interaction between species and framing for the first and the second GLMs, respectively. For the latter GLM, the framing was the factor chosen as the intercept.

For the two previous GLM pairs, we used data of both intact and treated inflorescences. The strength of the associations is expressed by non-transformed estimates. Values higher and lower than 0 connote positive and negative associations, respectively. Values above 0 indicate that pollinators more often visit inflorescences with decorative flowers and would be consistent with our hypothesis.

Lastly, a third GLM pair with a binomial distribution was used to determine whether decorative flowers function as landing-sites from observations of the number of initial pollinator landings, either on decorative or fertile flowers. For this last model pair, the response variable was the number of first landings to decorative and to fertile flowers. The predictor variables were the area of the decorative flowers relative to the total area of their inflorescences and the interaction between species and the relative area of decorative flower for the first and the second GLMs, respectively. For the latter GLM, the relative area of decorative flowers was the factor chosen as the intercept.

For this last GLM pair, we only used data on framed inflorescences (i.e. intact inflorescences of FR species, treated inflorescences of n-FR species). The strength of the associations is expressed by log-odds, log of odds ratios which represents the constant effect of a predictor on the likelihood that one outcome will occur. Values higher and lower than 0 connote positive and negative associations, respectively. Values above 0 indicate that pollinators land more frequently on decorative flowers and would be consistent with our hypothesis.

GLMs were adjusted using the R package ‘dispmod’ (functions: `glm.binomial.disp`; Scrucca 2018) to account for overdispersion. R^2 values were calculated for each GLM using the R package ‘rsq’ (function: `rsq`; Zhang 2018). The second GLM of each pair were plotted using the R package “sjPlot” (function: `plot_model`; Lüdtke 2018)

Results

Flowering biology and insect visitors

The *Hydrangea* species bloom from spring to late summer (supplementary Table S1). Anthesis of fertile flowers starts in the morning, and the flowers usually shed most of their pollen grains within one or a few days. Among the studied species, *H. sikokiana* had the highest number of fertile flowers per inflorescence and *H. luteovenosa* had the lowest (Table 1).

The main floral reward from visiting *Hydrangea* spp. was pollen. Nectar was only detected in fertile flowers of *H. paniculata* and *H. petiolaris*, with sugar concentrations of 50.0% and 31.2%, respectively. The nectar-probing behaviour of some insects on *H. scandens* and *H. luteovenosa* flowers suggests that fertile flowers of these plant species also secrete nectar (supplementary Fig. S1). Inflorescences of *H. hirta*, *H. paniculata*, and *H. petiolaris* had sweet odours.

Function of decorative flowers

From the first GLM pair, which tested whether framing increased the frequency of pollinator visits, the first GLM ($R^2 = 0.08$, $F_{(1, 106)} = 8.42$, dispersion = 0.591) revealed a significant positive association between framing and visitation rates (estimate = 1.97, $t = 18.87$, $P < 0.01$), supporting our prediction that decorative flowers increase the frequency of pollinators visits. The second GLM ($R^2 = 0.75$, $F_{(9, 90)} = 5.07$, $P < 0.001$) revealed positive associations for all species, significant only for *H. macrophylla*, *H. scandens* and *H. luteovenosa* (Fig. 2).

From the second GLM pair, which tested whether the total area of inflorescences increased the frequency of pollinator visits per area, the first GLM ($R^2 = 0.01$, $F_{(1, 94)} = 116.52$, dispersion = 0.736) revealed a non-significant negative association between framing and adjusted visitation rates (estimate = -0.14, $t = -0.82$, $P = 0.41$), contrary to our prediction that decorative flowers increase the

frequency of pollinators visits per unit area. The second GLM ($R^2 = 0.24$, $F_{(8, 80)} = 1.72$, $P = 0.11$) revealed non-significant positive associations for *H. scandens*, *H. luteovenosa* and *H. petiolaris*, and negative associations for the other studied species, only significant for *H. hirta*. (Fig. 3).

Lastly, from the third GLM pair, which tested whether decorative flowers functioned as landing-sites, the first GLM ($R^2 = 0.12$, $X^2 = 9.30$, $df = 1$, adjusted dispersion = 1) revealed a significant positive association between landings in decorative flower and the area of these flowers relative to the total area of their inflorescences (estimate = 2.38, $Z = 2.92$, $P < 0.01$), agreeing with our prediction that decorative flowers function as landing-sites for pollinators. The second GLM ($R^2 = 0.88$, $X^2 = 24.52$, $df = 8$, $P < 0.01$) revealed positive associations for *H. scandens*, *H. macrophylla*, *H. luteovenosa* and *H. serrata*, significant for the last two mentioned species, and non-significant negative associations for the other studied species (Fig. 4).

Discussion

Our results support the premise that the sacrifice of fertile flowers to produce decorative flowers provides an advantage to pollination success, namely, increasing the attractiveness of inflorescences to pollinators. The results show that decorative flowers of the studied *Hydrangea* species boost attractiveness to pollinators by increasing the inflorescence-surface area, but the attractiveness does not increase per unit area, and function as landing-sites only in certain species.

Our findings were consistent with the hypothesis that decorative flowers increase pollinator visitation rates, and this effect was most prominent for *H. luteovenosa*, *H. scandens* and *H. macrophylla*. These findings were similar to those of prior studies on species with framed inflorescences (Jin et al. 2010) and species with inflorescences with fertile and sterile flowers (Bell 1985; Andersson 1991, 2008; Celedón-Neghme et al. 2007; Morales et al. 2013). A combination of the following types of visual signals may be responsible for the increased attractiveness of framed inflorescences: First, an enlarged inflorescence area created by decorative flowers; second, an emphasized contrast between decorative flowers and the cluster of fertile flowers, and/or the

background (especially in coloured species); and third, a more complex silhouette created by the decorative flowers, namely a high contour intensity. While in general insect pollinators respond positively to the first visual signal type, an enlarged inflorescence area (Wyatt 1982; Brody and Mitchell 1997), the latter two types have been documented to be especially appealing to bees (Prokopy and Owens 1983; Conner and Rush 1996; Goulson 2000; Spaethe et al. 2001; Makino et al. 2007; Willmer 2011), although their effects on dipterans and coleopterans are not well known. This study only gives insight for the first visual signal types. Further studies on the effect of an emphasized contrast and a complex silhouette on the frequency of pollinator visits and pollination success will help clarify how pollinators respond to decorative flowers.

The results suggest that the large cluster of fertile flowers of *H. sikokiana* constitutes a sufficiently attractive visual signal, enough to limit the use and development of decorative flowers. If this is the case, the decorative flowers of *H. sikokiana* should be vestigial, since they are sterile and do not attract additional pollinators. As noted for other plant species by Ornduff (1969) and Eckert (2002), it is possible that the reduction in size and, plausible, vestigialization of *H. sikokiana* decorative flowers is related to self-pollination.

Our analysis does not support the hypothesis that decorative flowers function as landing-sites except for *H. serrata* and *H. luteovenosa*, species which share only few decorative flower traits. It is plausible that decorative flowers of certain *Hydrangea* species have evolved traits to function as landing-sites not considered in this study. For instance, conical cells, which facilitate pollinator gripping to the flowers (Whitney et al. 2009; Alcorn et al. 2012) and have been mainly recorded for petal surfaces (Christensen and Hansen 1998), may have appeared in sepals of decorative flowers of some *Hydrangea* species. There is little research related to the landing phenomenon in general. Further studies to discriminate the circumstances where decorative flowers and other flower organs, function as landing-sites will enhance our understanding of the functional properties of these floral organs in *Hydrangea* and plants with similar inflorescences.

The absence of decorative flowers in *H. hirta* might be related to the presence of other pollinator attracting traits: purple-coloured fertile flowers, colour attractive to various insect pollinators and particularly bees (Kevan and Baker 1983; Chittka and Thomsom 2001; Willmer 2011), and a strong floral odour. These traits might have sufficed to attract enough pollinators and restricted the use or evolution of decorative flowers, resulting in their loss or absence, respectively. However, this is likely not the case for the other n-FR *Hydrangea* species (i.e. *Hydrangea lingii* C. Ho, *Hydrangea serratifolia* (Hook. & Arn.) F.Phil. and *Hydrangea steyermarkii* Standl.), since only fertile flower of *H. hirta* are coloured, while white or pale-yellow in the other species, and the loss of decorative flowers is suggested to have occurred independently in the genus (Hufford 1997; Jacobs 2010).

From the results, we presume that clusters of fertile flowers alone, most notable for *H. hirta* and *H. sikokiana*, may attract insect pollinators by themselves, as shown for *Jacobaea vulgaris* by Andersson (1996) and *Cephalanthera falcata* by Suetsugu et al. (2015). In n-FR species, the attractiveness of their cluster of fertile flowers may be related to the loss of decorative organs, such as decorative flowers, as suggested by Andersson (1991). However, since pollinators, whether attracted by decorative flowers or the cluster of fertile flowers, forage for pollen and nectar on the fertile flowers (supplementary Fig. S1), it is likely that decorative flowers increase pollen import/export rates on fertile flowers. Considering the above-mentioned advantage of decorative flowers and that they possibly limit mating costs, in a similar fashion as the sterile flowers of *Leopoldia comosa* (L.) Parl. (Asparagaceae) (Morales et al. 2012), we expect decorative flowers should be under selective pressure.

Since the area of decorative flowers can be as large as the area of many fertile flowers, pollen transfer rates within a framed inflorescence ought to be lower when compared to an inflorescence of similar size and composed only of fertile flowers; a few decorative flowers replacing numerous fertile flowers likely reduce geitonogamy risks to a certain degree in FR species. It is possible that decorative flowers, in addition to their previously presented functions, also function to lower geitonogamy risks. This assumption is similar to that of Morales et al. (2012) for the sterile flower of *Leopoldia comosa*.

However, further research is still needed to understand whether and how decorative flowers influence pollen import/export within an inflorescence.

To conclude, our study is the first to show that decorative flowers of *Hydrangea* species increase the frequency of pollinator visits to inflorescences and that insect pollinators prefer to land on decorative flowers of at least certain species. Results suggest the decorative flowers have evolved mainly to boost attractiveness to pollinators. It is likely that *Hydrangea* species without and with pseudo-vestigial decorative flowers (as in *H. hirta* and *H. sikokiana*, respectively) have adopted other pollinator attraction strategies. An interesting approach for future studies, aside from the ones previously mentioned, would be to study the absence of decorative flowers. For instance, the importance of self-fertilization on the absence of decorative flowers. This importance is suggested by Lloyd (1987) and Goodwillie et al. (2010) based on the idea that attractive structures of plants, such as decorative flowers, should be reduced or lost in self-fertilizing species to allocate resources to fruit/seed set.

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Tables

Table 1. Features of the nine studied *Hydrangea* species, their decorative flowers and fertile flowers.

<i>Hydrangea</i> species (species code)	Inflorescence		Surface area (mean \pm SD, cm ²) (N=6)	Decorative flowers		Cluster of fertile flowers		Relative surface area of cluster of fertile flowers vs decorative flowers (mean \pm SD, %) (N=6)
	Type of inflorescence	Type of framing		Range of flowers per inflorescence ^b	Color	No. of flowers per inflorescence (mean \pm SD) (N) ^c	Color	
FR species								
<i>H. macrophylla</i>	compound corymb	complete	86.8 \pm 9.6	6–11 [8]	pale blue	170 \pm 24 (6)	blue	40.5 \pm 4.1
<i>H. serrata</i>	compound corymb	complete	50.8 \pm 6.2	4–10 [8]	blue	226 \pm 30 (7)	pale blue	57.7 \pm 5.2
<i>H. involucrata</i>	compound corymb	loose	48.5 \pm 3.8	6–17 [8]	white	246 \pm 32 (7)	pale purple	60.6 \pm 2.0
<i>H. petiolaris</i>	compound corymb	loose	55.2 \pm 3.0	4–11 [8]	white	420 \pm 57 (8)	white	70.9 \pm 2.1
<i>H. sikokiana</i>	compound corymb	loose	230.8 \pm 6.9	4–10 [8]	white	676 \pm 64 (6)	white	91.0 \pm 1.9
<i>H. scandens</i>	corymb	partial	22.1 \pm 2.4	2–5 [4]	white	32 \pm 6 (10)	white	41.9 \pm 2.0
<i>H. luteovenosa</i>	corymb	partial	6.8 \pm 0.6	2–4 [2]	white	11 \pm 2 (12)	white	32.9 \pm 1.8
<i>H. paniculata</i>	compound panicle	complete ^a	—	6–16 [8–12]	white	332 \pm 60 (7)	white	—
n-FR species								
<i>H. hirta</i>	compound corymb	not framed	38.4 \pm 4.5	0 [4]	purple	95 \pm 6 (6)	pale purple	25.6 \pm 2.8

FR species, framed species; n-FR species, non-framed species.

^a Decorative flowers of *H. paniculata* completely framed the inflorescences when looked from the apical proportion of the panicle. Surface area of this species was not calculated due to its panicked inflorescence.

^b Range observed in the observed population of *Hydrangea* species. Number in brackets is the number of decorative flowers in observed framed inflorescences. For *H. hirta* we mounted purple decorative flowers from a *H. macrophylla* cultivar.

^c The number of fertile flowers was counted from some of the inflorescences used to observe insect visits.

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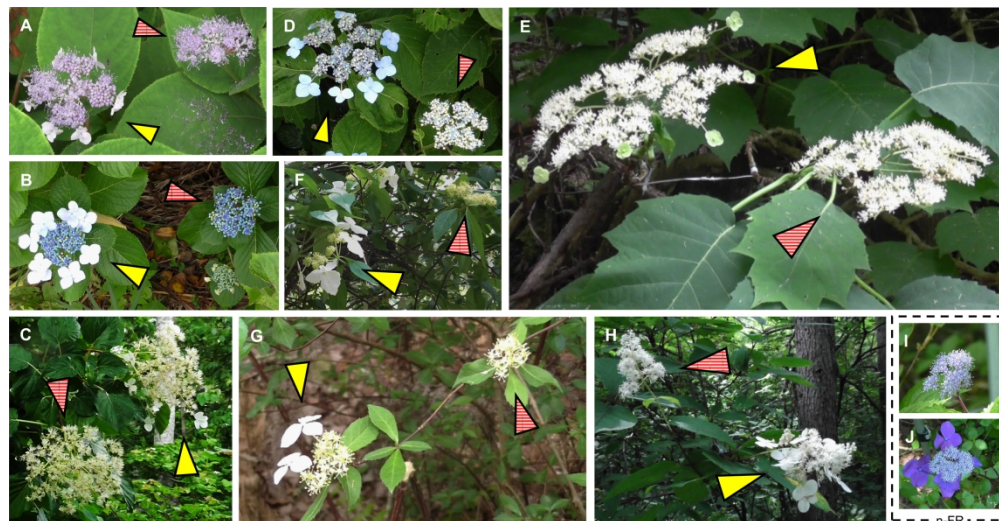
Figure Captions

Fig. 1. Intact and treated inflorescences of nine *Hydrangea* species. (A) *H. involucrata*; (B) *H. macrophylla*; (C) *H. petiolaris*; (D) *H. serrata*; (E) *H. sikokiana*; (F) *H. scandens*; (G) *H. luteovenosa*; (H) *H. paniculata*; (I) intact inflorescence of *H. hirta*; and (J) treated inflorescence of *H. hirta*. In species with inherent decorative flowers: red striped arrows, treated inflorescences; yellow solid arrows, intact inflorescences. Decorative flowers were clipped in framed species and mounted on non-framed species. In *H. hirta*, we mounted decorative flowers of a purple *H. macrophylla* cultivar. n-FR species, non-framed species.

Fig. 2. Estimated associations between framing and visitation rates to nine *Hydrangea* species. The t and P values were calculated from the interaction terms of the model. Error bars show the 95% confidence intervals estimates of each GLM term. Model dispersion = 0.275. ‘*’ $P < 0.05$; ‘**’ $P < 0.01$; ‘***’ $P < 0.001$; ‘†’, non-framed species.

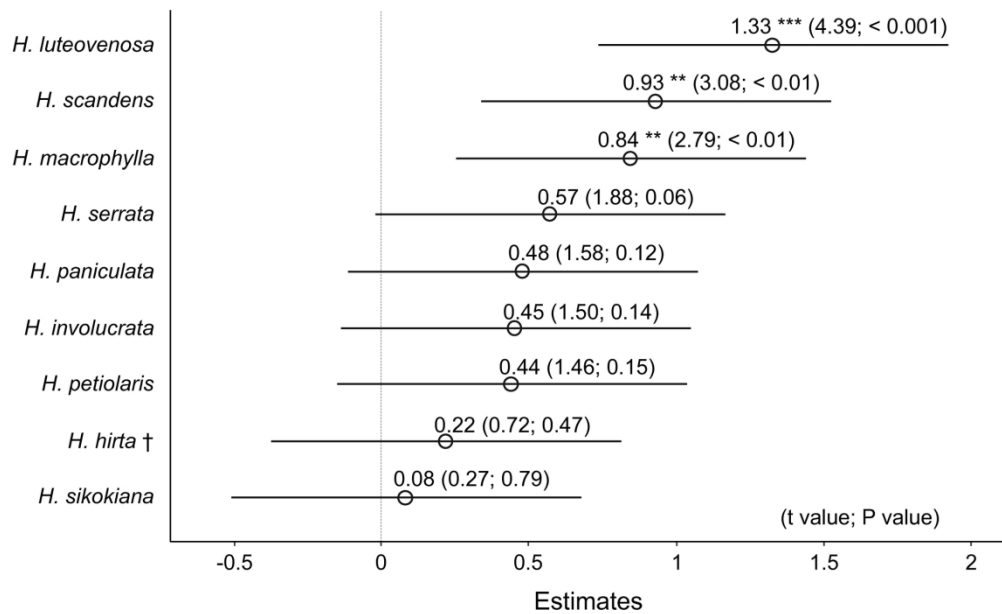
Fig. 3. Estimated associations between inflorescence-surface area and adjusted visitation rates to eight *Hydrangea* species. The t and P values were calculated from the interaction terms of the model. Error bars show the 95% confidence intervals estimates of each GLM term. Model dispersion = 0.658. ‘*’ $P < 0.05$; ‘**’ $P < 0.01$; ‘***’ $P < 0.001$; ‘†’, non-framed species.

Fig. 4. Estimated associations between number of landings and flower types of eight *Hydrangea* species. The Z and P values were calculated from the interaction terms of the model. Error bars show the 95% confidence intervals of Log-odds of each GLM term. Model dispersion = 1.315. ‘*’ $P < 0.05$; ‘**’ $P < 0.01$; ‘***’ $P < 0.001$; ‘†’, non-framed species.



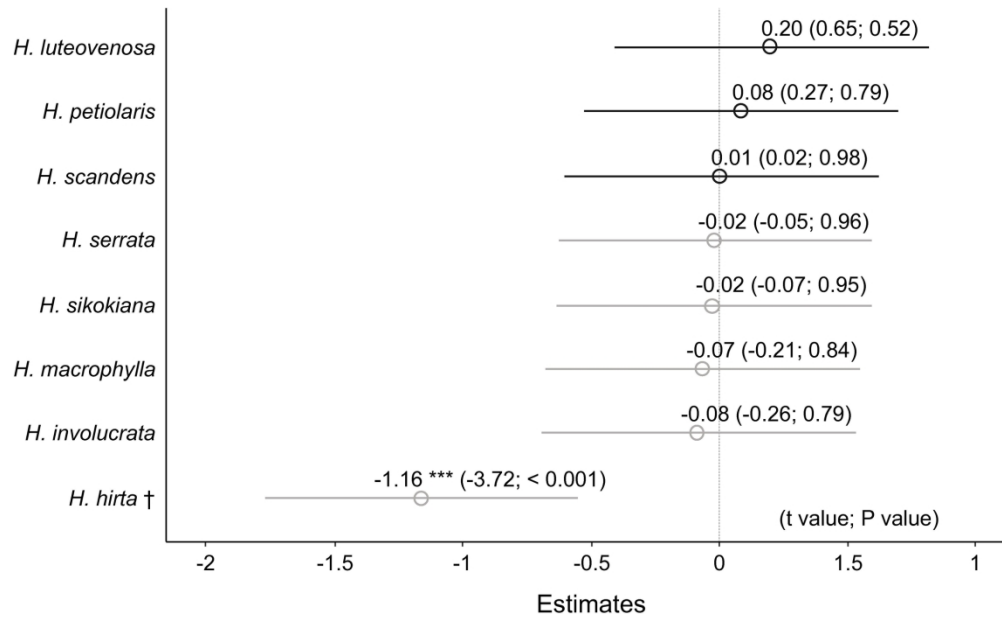
Intact and treated inflorescences of nine *Hydrangea* species. (A) *H. involucrata*; (B) *H. macrophylla*; (C) *H. petiolaris*; (D) *H. serrata*; (E) *H. sikokiana*; (F) *H. scandens*; (G) *H. luteovenosa*; (H) *H. paniculata*; (I) intact inflorescence of *H. hirta*; and (J) treated inflorescence of *H. hirta*. In species with inherent decorative flowers: red striped arrows, treated inflorescences; yellow solid arrows, intact inflorescences. Decorative flowers were clipped in framed species and mounted in non-framed species. In *H. hirta*, we mounted decorative flowers of a purple *H. macrophylla* cultivar. n-FR species, non-framed species.

253x133mm (300 x 300 DPI)



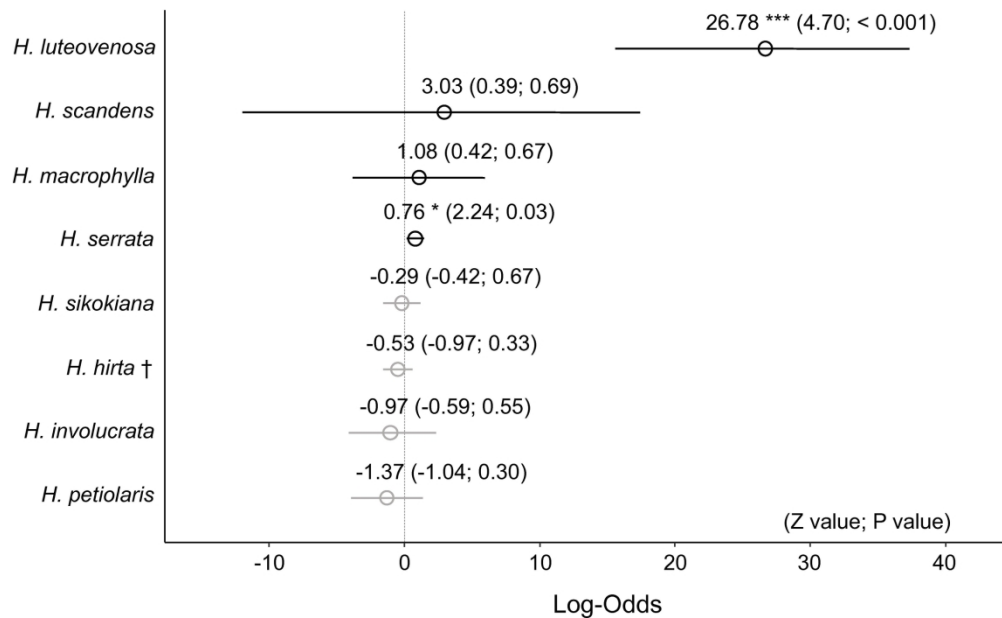
Estimated associations between framing and visitation rates to nine *Hydrangea* species. The t and P values were calculated from the interaction terms of the model. Error bars show the 95% confidence intervals estimates of each GLM term. Model dispersion = 0.275. *' $P < 0.05$; '**' $P < 0.01$; '***' $P < 0.001$; '†', non-framed species.

198x119mm (300 x 300 DPI)



Estimated associations between inflorescence-surface area and adjusted visitation rates to eight *Hydrangea* species. The *t* and *P* values were calculated from the interaction terms of the model. Error bars show the 95% confidence intervals estimates of each GLM term. Model dispersion = 0.658. '*' *P* < 0.05; '**' *P* < 0.01; '***' *P* < 0.001; '†', non-framed species.

197x119mm (300 x 300 DPI)



Estimated associations between number of landings and flower types of eight *Hydrangea* species. The *Z* and *P* values were calculated from the interaction terms of the model. Error bars show the 95% confidence intervals of Log-odds of each GLM term. Model dispersion = 1.315. '*' *P* < 0.05; '**' *P* < 0.01; '***' *P* < 0.001; '†', non-framed species.

197x120mm (300 x 300 DPI)