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The pistil as a traffic light: Yellow-to-red color change likely influences pollinator visitation patterns in *Saxifraga fortunei* (Saxifragaceae)

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Societal Impact Statement

Flowers can communicate reproductive status to pollinators through visual cues. In *Saxifraga fortunei*, pistils often changed from yellow to red after pollination, and hoverflies and honeybees preferentially visited flowers with yellow pistils. This pattern suggests that a post-pollination color shift confined to the pistil can reduce revisits to already pollinated flowers and concentrate visitation on flowers still capable of seed set, thereby improving pollination efficiency in dense floral displays. These findings broaden current views of floral signaling by demonstrating that a floral organ other than the perianth can function as a dynamic visual cue.

Summary

- Floral color change during anthesis has been documented in many angiosperms and is widely regarded as a visual signal influencing pollinator visitation. Nevertheless, direct empirical evidence remains scarce, and no study has demonstrated that color change confined to floral organs other than petals or sepals is associated with pollinator visitation patterns.
- We investigated pistil color change in *Saxifraga fortunei* by assessing its association with pollinator activity in natural populations and laboratory hand-pollination and wounding experiments. We also surveyed floral morphology in closely related taxa through field observations, literature review, and online image databases.
- In *S. fortunei*, pistils often changed from yellow to red after pollination, and reddened pistils consistently showed pollen tubes reaching the ovules, whereas yellow pistils often exhibited incomplete or absent pollen tube growth. Field observations showed that hoverflies and honeybees visited only flowers with yellow pistils, a pattern suggesting that pistil color change underlies reduced visitation following pollination and may enhance pollination efficiency. Comparative surveys revealed that similar pistil color change occurs in several related species, suggesting that they may share the same pollination strategy as *S. fortunei*.

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- Overall, our study provides the first empirical evidence that color change restricted to the pistil is associated with changes in pollinator visitation and highlights previously overlooked roles of non-perianth floral organs in plant–pollinator interactions. Further investigation is needed to clarify how this trait evolved and diversified among related taxa.

KEYWORDS

floral color change, pistil color change, pistil reddening, pollinator visitation patterns, *Saxifraga fortunei*, *Saxifraga* sect. *Irregulares*

1 | INTRODUCTION

The coloration of angiosperm flowers has evolved to align with the sensory characteristics of their primary pollinators, most often insects with species-specific visual systems, thereby enhancing pollinator attraction (Fenster et al., 2004; van der Kooi et al., 2021). Because pollinators visit flowers in search of rewards such as nectar and pollen, floral coloration can enhance pollination efficiency by signaling the location of these rewards (McEwen & Vamosi, 2010; van der Kooi et al., 2019). Patterns of floral coloration vary among taxa, with some species accentuating particular floral organs such as petals and the gynoecium, whereas others exhibit color patterning (e.g., spots and gradients) that directs pollinators toward reward sites (Kevan & Backhaus, 1998; Leonard & Papaj, 2011; van der Kooi et al., 2019, 2021).

Another strategy for directing pollinator visitation toward fresh, highly fertile, or unpollinated flowers is floral color change during anthesis. Such changes are widespread among angiosperms: Flowers initially present colors that attract pollinators and subsequently shift to less attractive colors (Rezende et al., 2025; Weiss, 1995; Weiss & Lamont, 1997). This shift is considered a mechanism that deters pollinators from visiting flowers whose reproductive capacity has declined with age or that have already been pollinated (Weiss, 1995; Weiss & Lamont, 1997). Floral color change can occur in different organs depending on the species, including entire petals or sepals, localized petal or sepal regions, the calyx, androecium, gynoecium, or combinations of these structures (Ohashi et al., 2015; Weiss, 1995). Despite the many species that exhibit floral color change, relatively few studies have shown through field observations or experimental manipulation that these changes influence pollinator visitation patterns. Moreover, most studies have focused on cases in which color change occurs in petals or sepals, either alone or together with other organs (e.g., Brito et al., 2015; Delph & Lively, 1985, 1989; Ida & Kudo, 2010; Lim & Burns, 2024; Pereira et al., 2011; Santana et al., 2022). To date, no study has shown that color change confined to a single floral organ other than petals or sepals, such as the gynoecium, is associated with pollinator visitation patterns.

In *Saxifraga fortunei* (Saxifragaceae), flowers with yellow pistils and those with red pistils occur simultaneously on the same individual during anthesis (Figure 1a). Previous work has reported frequent visitation by hoverflies and honeybees (Negoro, 2005; Tanaka, 1983).

Because hoverflies often prefer yellow and show low sensitivity to longer red wavelengths (An et al., 2018; Ilse, 1949; Neimann et al., 2018; van der Kooi et al., 2021), *S. fortunei* may modulate pollinator visitation patterns through pistil color change. Accordingly, this study aimed to determine (i) whether pistil color in *S. fortunei* changes during anthesis and what factors trigger this change and (ii) whether pistil color change is associated with pollinator visitation patterns. Additionally, based on literature review, field observations, and online surveys of floral morphology in related species, we discuss how the focal species may have evolved pistil color change as a mechanism for regulating pollinator visitation.

2 | MATERIALS AND METHODS

2.1 | Study species and study sites

S. fortunei s.l. (Saxifragaceae) is a perennial herb widely distributed across East Asia and classified within sect. *Irregulares*, which is characterized by zygomorphic flowers (Magota, Sakaguchi, Lee, et al., 2021; Pan et al., 2001; Tkach et al., 2015; Wakabayashi, 2001; Zhang et al., 2020). Although several infraspecific taxa have been described based on morphology, habitat preference, and related traits (Hara, 1935; Nakai, 1938, 1953; Wakabayashi, 2001), many of them do not reflect genetic relationships, and taxonomic boundaries remain unresolved (Magota, Sakaguchi, Lee, et al., 2021).

S. fortunei var. *suwoensis* occurs in riparian habitats in Japan and is characterized by orbicular leaves with a cordate base that are palmately divided into five to seven lobes (Nakai, 1953; Wakabayashi, 2001; Fujii et al., 2020; Magota, Sakaguchi, Lee, et al., 2021; Figure 1a). Field surveys were conducted each October from 2023 to 2025 in a natural flowering population of *S. fortunei* var. *suwoensis* (hereafter *S. fortunei*) in the Tanjō Mountains, Kita-ku, Kobe-shi, Hyogo Prefecture, Japan (34°47'N, 135°11'E). The site is a temperate broad-leaved secondary forest along a stream at approximately 500-m elevation in a rhyolitic region. Plants grow on exposed rhyolite or shallow soil over bedrock, and about 1000 individuals flower annually from late September to early November. Laboratory experiments, including pollination treatments, used three individuals cultivated in an incubator (12 h light at 20°C; 12 h dark at 15°C) and 20 individuals grown to flowering in an unheated greenhouse.

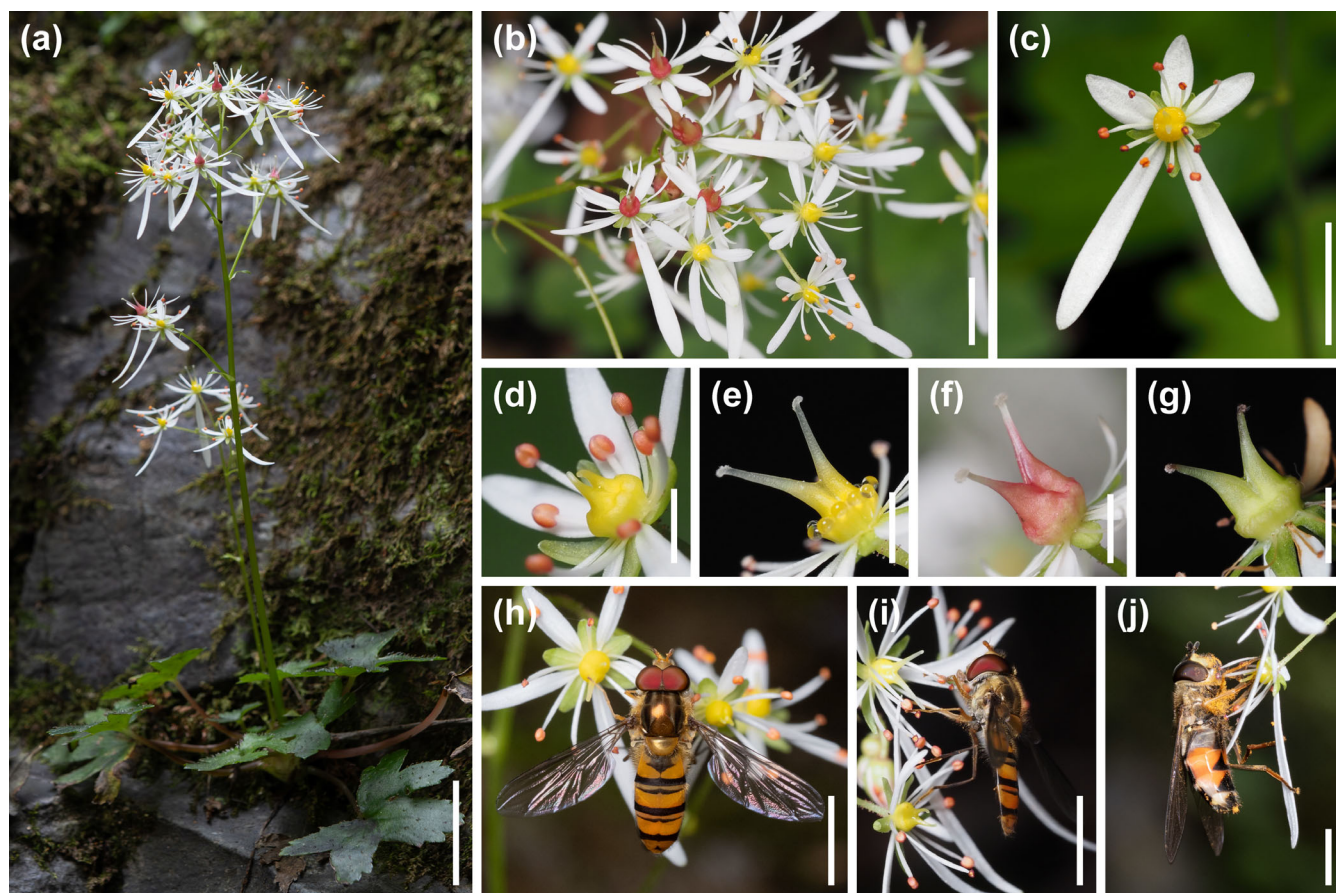


FIGURE 1 *Saxifraga fortunei* var. *suwoensis* and its pollinators. (a) Flowering plant. (b) Close-up of the inflorescence showing both yellow and red pistils. (c) Flower in the male phase. (d) Yellow pistil with immature stigmas (male phase). (e) Yellow pistil with mature stigmas (female phase). (f) Red pistil with mature stigmas (female phase). (g) Green, immature fruits. (h, i) *Episyrphus balteatus* visiting a flower. (j) *Eupodes corollae* visiting a flower. Scale bars: 3 cm (a), 1 cm (b, c), 3 mm (d–g), and 5 mm (h–j). Photographs by Kazuma Takizawa.

2.2 | Plant phenology and pistil color change

Although *S. fortunei* is expected to exhibit pistil color change during anthesis, its flowering phenology and the timing of color transitions have not been described in detail. Between 15 and 28 October 2023, we monitored flowering from anthesis to early fruit development in wild plants from the study population and in cultivated individuals grown under controlled conditions, documenting sequential changes in floral traits and coloration. We also assessed the distribution of pollinator-visible ultraviolet reflectance across floral organs in cultivated plants using a modified camera. Images were obtained with a Sony NEX-5 (Sony, Japan) from which the low-pass filter had been removed, equipped with an SEL30M35 E 30-mm F3.5 Macro lens (Sony, Japan) and a UV-pass filter transmitting only 320- to 380-nm light (Baader U-Venus Filter, Baader Planetarium, Germany).

To test whether pollination is associated with pistil color change, on 24 October 2024 and 21 October 2025, we randomly collected 16 flowers with yellow pistils and 16 flowers with red pistils from wild plants during the female phase and fixed them in FAA (60%

ethanol:formalin:acetic acid = 90:5:5). Pistils were excised, softened in 1 M KOH at 60°C for 30 min, rinsed twice in distilled water, and stained with 0.1% aqueous aniline blue for 1.5 h at room temperature. Stained pistils were mounted in 50% glycerol, and pollen tube growth was examined using the squash method under a fluorescence microscope (BX-60, Olympus Corporation, Japan). Among 16 flowers with yellow pistils, we examined 11 flowers in which pollen grains were confirmed on the stigma under microscopic observation. The remaining five flowers with yellow pistils lacked pollen grains on the stigma and were therefore not assessed for pollen tubes (Dataset S2).

2.3 | Pollinator observations

Pollinator identification and behavioral observations were conducted in the natural study population described above during October 2023, 2024, and 2025, on six non-rainy days between 10:00 and 16:00, totaling 12.5 h (Dataset S1). Insects visiting *S. fortunei* flowers were collected and examined for pollen on their body surfaces. The

behavior of hoverflies and honeybees, the most frequent pollinators, was recorded on video for 2656 and 42 s, respectively. The total video duration exceeded the summed visitation time because it included intervals when insects were absent from flowers or moving between flowers. Recordings were made at 30 fps using one of the following devices: OM-D E-M5 Mark III (OM Digital Solutions, Japan) with M. Zuiko Digital ED 12- to 100-mm F4.0 IS PRO (OM Digital Solutions, Japan), OLYMPUS Tough TG-6 (OM Digital Solutions, Japan), iPhone 16 Pro (Apple Inc., United States), or iPhone 13 (Apple Inc., United States). A visit was defined as an insect remaining on the same flower for at least 1 s. Pollinator preference for flowers with yellow versus red pistils was assessed using 80 hoverfly visits and 10 honeybee visits, and deviations from equal preference were tested using binomial tests. Because honeybee visits were infrequent during the observation periods, the number and duration of honeybee recordings were limited relative to those of hoverflies. Using hoverfly residence times on male- and female-phase flowers with yellow pistils (58 and 22 visits, respectively), differences between sexual phases were evaluated using Welch's t-test.

2.4 | Hand-pollination and wounding treatments

Floral color change may be induced by pollination, senescence, or other physiological processes (Ida & Kudo, 2010; Ram & Mathur, 1984; Santana et al., 2022; Zhang et al., 2012). Anthocyanins, which contribute to red pigmentation in floral tissues, are also synthesized in response to stresses such as herbivory, pathogen attack, high light, and drought (Chalker-Scott, 1999; Gould, 2004; Steyn et al., 2002). To identify factors responsible for pistil color change in *S. fortunei*, hand-pollination and wounding experiments were performed from 11 October to 2 December 2024 and from 15 October to 12 December 2025. Flowers that opened in the incubator or greenhouse were assigned to one of the following treatments: (i) hand cross-pollination (pollen from a different individual applied to female-phase flowers after anther removal; $n = 25$), (ii) hand self-pollination (pollen from the same individual applied after anther removal; $n = 33$), (iii) emasculation (anthers removed without pollination; $n = 12$), (iv) wounding during the male phase (the pistil or nectary disk pricked with a needle; $n = 5$), (v) wounding during the female phase (the pistil or nectary disk pricked; $n = 5$), and (vi) control (no treatment from anthesis to senescence; $n = 88$). Flowers were examined daily for pistil color change, which was categorized as strong reddening (the entire pistil uniformly deep red), weak reddening (the entire pistil reddened but pale and retaining a greenish component), or reddening restricted to the nectary disk (reddening confined to the nectary disk only). Greenhouse plants were enclosed with nets to exclude insect visitors. For treatments (i) and (ii), flowers that failed to set fruit were excluded. For treatments (iii) to (vi), flowers exhibiting reddening were examined for pollen tube growth, and those with pollen tubes were excluded because accidental pollination was inferred.

2.5 | Floral morphology and pistil color change in related species

In addition to *S. fortunei* var. *suwoensis*, we examined other infraspecific taxa and closely related species, particularly within sect. *Irregulares*, through literature review, field observations, and online image databases.

For each taxon, we recorded petal color and pattern, pistil color at anthesis, the presence or absence of pistil color change and the resulting color, the frequency and timing of color change, and capsule coloration. We primarily consulted taxonomic monographs and regional floras, supplemented by species-specific publications. Because information on petal pattern and pistil coloration was often limited, we inferred these traits from figures and photographs when available. For several species, we conducted direct field observations. We also examined photographs associated with records in the citizen science database iNaturalist (<https://www.inaturalist.org>) and the Plant Photo Bank of China (PPBC; <https://ppbc.iplant.cn>). For taxa exhibiting pistil color change, we classified it as “common” when most flowers within an inflorescence exhibited color change and as “rare” when color change was exceptional, often limited to a single pistil.

3 | RESULTS

3.1 | Plant phenology and pistil color change

Observations showed that *S. fortunei* produces protandrous, hermaphroditic flowers (Figure 1a–c). Pollen is released at anthesis during the male phase (Figure 1d), after which the stigma matures and becomes receptive in the female phase (Figure 1e). All pistils were yellow at the onset of anthesis (Figure 1d). Although stigma maturation occurred while pistils remained yellow (Figure 1e), some pistils turned red only after stigma maturation (Figure 1f). As petals and stamens senesced and fruit development began, the red coloration faded and pistils turned green (Figure 1g). Ultraviolet imaging showed that yellow pistils were UV-reflective throughout both sexual phases (Figure S1a,b), whereas red pistils were UV-absorbing (Figure S1c). In both the visible and ultraviolet wavelength ranges, no color change was detected in any floral organ other than the pistil, and petals showed no conspicuous patterning (Figure S1).

Among pistils collected from the natural population, pollen tube growth was detected in seven of 11 yellow pistils, and in five of these cases, pollen tubes reached the ovules (Dataset S2). In contrast, all red pistils ($n = 16$) showed pollen tube growth, with pollen tubes reaching the ovules. The degree of pistil reddening varied markedly among individuals (Dataset S2). Some pistils exhibited intense reddening across the entire pistil (Figure 2a), others showed weak overall reddening (Figure 2b), and some displayed reddening restricted to the nectary disk while other tissues turned green (Figure 2c). These patterns were generally consistent within individuals.

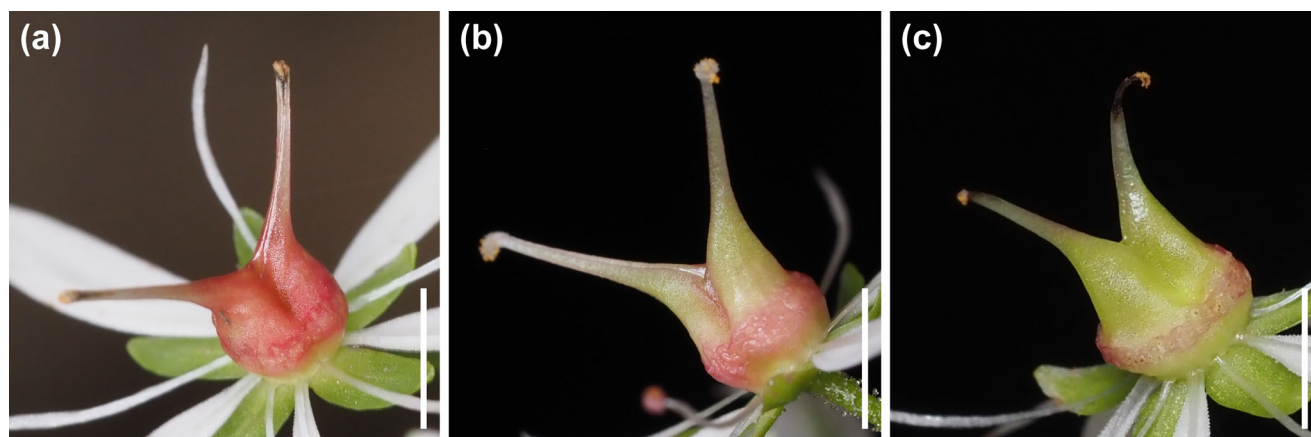
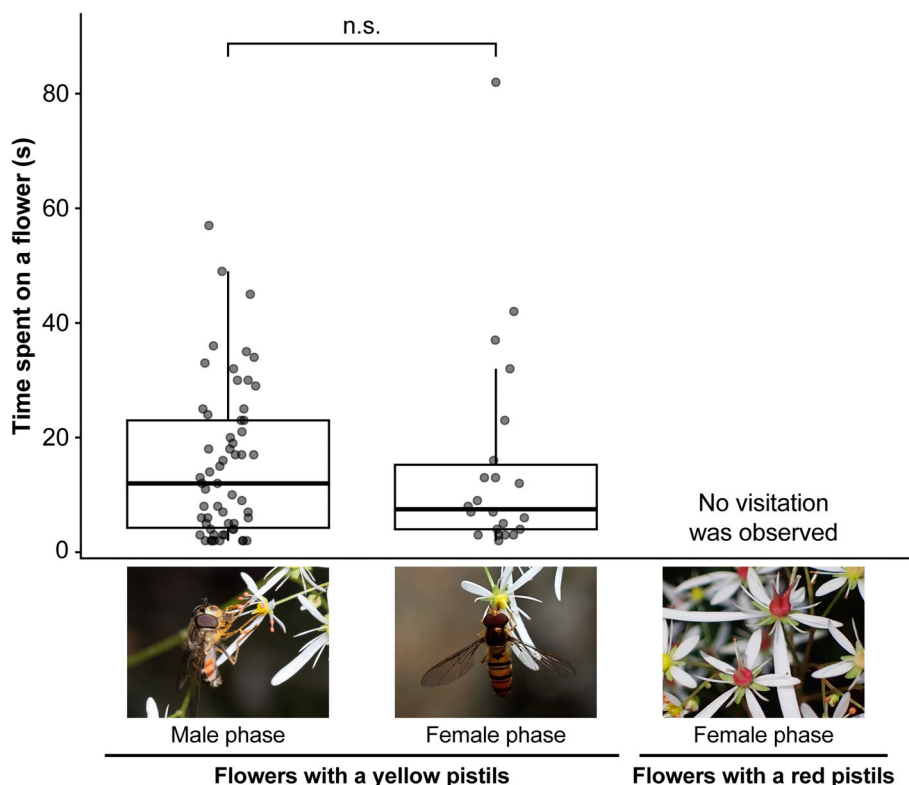


FIGURE 2 Variation in the degree of pistil reddening in *Saxifraga fortunei* var. *suwoensis*. (a) Pistil showing strong overall reddening. (b) Pistil showing weak overall reddening. (c) Pistil with reddening restricted to the nectary disc. Scale bars: 3 mm. Photographs by Kazuma Takizawa.

FIGURE 3 Hoverfly residence time per visit on *Saxifraga fortunei* flowers differing in sexual phase and pistil color. “n.s.” indicates no significant difference ($p > .05$). Photographs by Kazuma Takizawa (hoverfly visiting a male-phase flower with a yellow pistil and female-phase flowers with red pistils) and Takahiro Kimoto (hoverfly visiting a female-phase flower with a yellow pistil).



3.2 | Pollinators and their behaviors

In the natural population, the main floral visitors were *Episyrphus balteatus* (Figure 1h,j; >50 individuals), *Eupeodes corollae* (Figure 1j; >10 individuals), and *Apis cerana japonica* ($n = 5$), indicating that hoverflies, and possibly honeybees, function as the primary pollinators of *S. fortunei*, consistent with earlier studies (Negoro, 2005; Tanaka, 1983). These insects fed on pollen and lapped nectar, and pollination occurred when pollen adhering to their bodies contacted the stigma (Figure 1h–j). Honeybees were also observed actively collecting pollen.

Hoverflies and honeybees made 80 and 10 visits, respectively (Dataset S3). Total visitation time was 1226 s for hoverflies and 17 s for honeybees, reflecting relatively infrequent honeybee visitation during the observation periods. All recorded visits were to flowers with yellow pistils, and none were observed on flowers with red pistils (Figure 3). Binomial tests showed that visitation by both hoverflies and honeybees was strongly biased toward flowers with yellow pistils ($p < .001$ and $p < .01$, respectively). Among flowers with yellow pistils, hoverfly residence time per visit did not differ between male- and female-phase flowers ($p > .05$; Figure 3). Although honeybees were recorded less frequently and for shorter durations than hoverflies, the

consistent absence of visits to flowers with red pistils suggests that honeybee visitation is also likely biased toward flowers with yellow pistils. However, the limited number and duration of honeybee observations constrain direct comparisons of their overall pollination contribution with that of hoverflies.

3.3 | Breeding system and probable trigger for pistil color change

Hand-pollination experiments demonstrated that *S. fortunei* sets fruit following both self- and cross-pollination and that pollination is required for fruit production (Dataset S4). In the self- and cross-pollination treatments, 87.9% (29/33) and 72.0% (18/25) of pistils reddened, respectively. As in the natural population (Figure 2), substantial inter-individual variation was observed, including strong reddening (11/58), weak reddening (6/58), reddening restricted to the nectary disk (30/58), and pistils that did not redden despite successful fruit set but instead remained yellow during anthesis and later turned green (11/58).

In contrast, in treatments without pollination (emasculature, wounding, and control), pistils generally did not redden before floral senescence. Reddening restricted to the nectary disk occurred only rarely in unpollinated flowers (1/5 flowers in the female-phase wounding treatment and 13/88 flowers in the control group). All such cases lacked pollen tube growth and failed to produce fruit.

3.4 | Floral morphology and pistil color change in related species

S. fortunei var. *suwoensis* bears yellow pistils at anthesis that often turn red after pollination and later become green during fruit development (Figures 1d–g and 4a,e). In the alpine populations we examined, pistils of *S. fortunei* var. *alpina* remained red after petal abscission and throughout fruit maturation (Figure 4b,f and Table S1). Observations of a cultivated population at approximately 800-m elevation in the Rokko Alpine Botanical Garden, together with literature review and iNaturalist records, further indicate that var. *alpina* includes individuals with green capsules, as in var. *suwoensis*, as well as individuals whose capsules remain red (Figure 4c,g).

Across other species within sect. *Irregulares*, as well as related sections and genera, floral traits varied widely, particularly in petal patterning, pistil coloration, and the presence or absence of pistil color change (Figure 4 and Table S1). Most members of sect. *Irregulares* have white petals and yellow pistils at anthesis, but the occurrence of petal spots and pistil color change varies among species. Where pistil color change occurs, the most common transition is from yellow to red and typically occurs in most flowers within an inflorescence. In contrast, *S. cortusifolia* var. *cortusifolia* showed pistil reddening only rarely, and several species exhibited shifts to other colors or no pistil color change (Figure 4).

Species sharing the distinctive combination observed in *S. fortunei*, namely, white, unspotted petals and frequent pistil

reddening from yellow to red, were identified within sect. *Irregulares*, including *S. rufescens* and *S. serotina*. Similar trait combinations were also observed in actinomorphic species from other sections or genera, such as *S. mertensiana* and *Micranthes occidentalis* (Table S1).

4 | DISCUSSION

4.1 | Possible triggers of pistil color change

Field and laboratory observations showed that in *S. fortunei* the pistil often changes from yellow to red after successful pollination (Figure 1). Pollen tubes reached the ovules in all reddened pistils, whereas pollen tube progression in yellow pistils was variable. This pattern suggests that pistil reddening is triggered after pollen tubes reach the ovules and possibly after fertilization. Although reddening was generally induced by pollination, weak reddening occurred in a few unpollinated pistils. Because anthocyanins, the main red pigments, are also produced in response to stress factors such as herbivory, pathogen attack, high light, and drought (Chalker-Scott, 1999; Gould, 2004; Steyn et al., 2002), slight reddening in unpollinated pistils might reflect stress-induced responses.

The degree of reddening varied markedly among individuals, ranging from intense coloration across the entire pistil to faint or localized reddening, or nearly no reddening despite successful fruit set. Because individuals tended to show consistent patterns, this variation likely reflects environmental conditions or genetic background (Farzad et al., 2003; Fukada-Tanaka et al., 2000; Jabbari et al., 2013; Parrish et al., 2024). Consistent differences among infraspecific taxa within the *S. fortunei* complex, such as prolonged pistil reddening in alpine *S. fortunei* var. *alpina* (Figure 4b,f and Table S1), further suggest that environmental or genetic factors modulate the extent of color change. The extent of this variation should be assessed across additional populations of *S. fortunei* var. *suwoensis* and other infraspecific taxa. Elucidating the molecular and physiological mechanisms underlying pistil color change in *S. fortunei*, as well as the sources of individual variation, remains an important topic for future research.

4.2 | Adaptive significance of pistil color change

Our field observations and experiments show that pistil color change in *S. fortunei* is closely linked to pollination status and associated with shifts in pollinator visitation, with implications for reproductive efficiency. Pistils are yellow during anthesis and the receptive female phase and often turn red only after successful pollination and pollen tube growth to the ovules (Figure 1d–f), accompanied by a shift from UV-reflective to UV-absorbing (Figure S1). Hoverflies and honeybees, the pollinators in the study population, visited only flowers with yellow pistils and avoided those with red pistils. Because our visitation data are observational, we cannot exclude the possibility that nonvisual cues, such as floral scent or variation in reward availability, also contribute to this visitation bias. In densely flowering *S. fortunei*, it will be

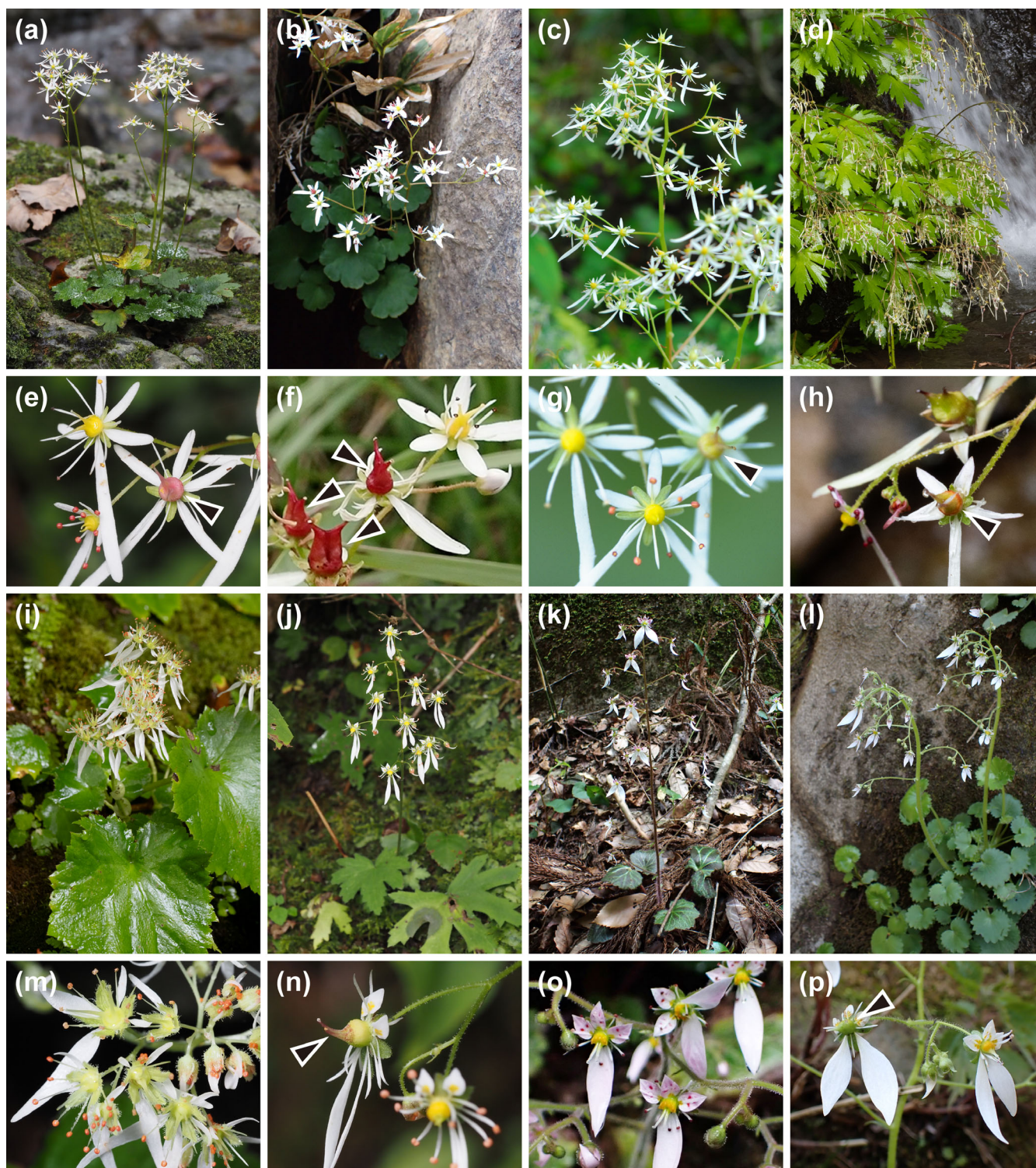


FIGURE 4 Floral morphology of *Saxifraga fortunei* and closely related species in sect. *Irregulares*. (a, e) *S. fortunei* var. *suwoensis*; a reddened pistil is indicated by the arrow in (e). (b, f) *S. fortunei* var. *alpina* from an alpine population; reddened pistils are indicated by arrows in (f). (c, g) *S. fortunei* var. *alpina* from a cultivated population; a reddened pistil is indicated by the arrow in (g). (d, h) *S. acerifolia*; reddened pistils are indicated by the arrow in (h). (i, m) *S. sendaica*; pistils show no color change during flowering. (j, n) *S. cortusifolia* var. *cortusifolia*; localized reddening is indicated by the arrow in (n). (k, o) *S. stolonifera*; pistils show no color change during flowering. (l, p) *S. nipponica*; a pistil that turned green is indicated by the arrow in (p). Photographs by Kazuma Takizawa (a, b, d–f, h–p) and Rokko Alpine Botanical Garden (c, g).

important to evaluate how such cues interact with visual signals to influence pollinator behavior (Raguso, 2008). In our experiments, reddening occurred primarily after pollination and pollen tube arrival at the ovules, suggesting that pistil color can act as a post-pollination cue that concentrates visitation on flowers still capable of seed set.

Most previous studies of floral color change have focused on petals, with fewer examining changes in the androecium or gynoecium. One of the few examples is *Tibouchina* (Melastomataceae), in which coordinated color change in petals, stamens, and style directs pollinators toward unpollinated flowers (Brito et al., 2015; Pereira et al., 2011). In contrast, to our knowledge, no previous study has demonstrated that color change restricted solely to the pistil during anthesis is associated with pollinator visitation. By linking pistil reddening with pollen tube arrival at ovule and pollinator visitation patterns in *S. fortunei*, this study highlights the functional importance of color change in floral organs beyond petals or sepals.

Floral color change occurs across diverse angiosperm lineages but is neither universal nor common (Ohashi et al., 2015; Ruxton & Schaefer, 2016; Weiss & Lamont, 1997). It entails substantial physiological costs, including pigment biosynthesis, pH regulation, and maintenance of floral tissues (Ashman & Schoen, 1994; Rezende et al., 2025). Many plants instead abscise old or pollinated flowers, thereby directing pollinator visitation toward newly opened ones (Ashman & Schoen, 1994). One hypothesis is that some species retain nonfunctional flowers because doing so enhances long-distance attraction, given that insects have limited spatial resolution and must approach closely to resolve small floral displays (Chittka & Raine, 2006; de Ibarra et al., 2015; Rigosi et al., 2017). Consistent with this idea, several studies have suggested or demonstrated that retaining older flowers increases floral display size and pollinator attraction, particularly in species with a single inflorescence (Brito et al., 2015; Gori, 1989; Kudo et al., 2007; Oberrath & Böhning-Gaese, 1999; Weiss, 1991).

However, frequent visitation to nonfunctional flowers reduces reproductive efficiency by diverting pollinators away from rewarding flowers. Once pollinators approach closely enough to discriminate color differences, they preferentially visit rewarding flowers that have not yet undergone color change (Chittka & Raine, 2006; Reverté et al., 2016; van der Kooi et al., 2021). In *S. fortunei*, dense clusters of white flowers create a conspicuous display, whereas pistil color change from yellow to red, accompanied by a shift from UV-reflective to UV-absorbing, is associated with increased visitation to unpollinated flowers that still offer rewards. These findings align with theoretical predictions that floral color change can offset the costs of retaining nonfunctional flowers while maintaining a large floral display.

4.3 | Possible origin of pistil color change

Our finding that pistil color change in *S. fortunei* is associated with pollinator visitation raises questions about the origin and function of this trait in related taxa. Our survey indicates that pistil reddening is widespread in *Saxifraga*, particularly within sect. *Irregulares*, but varies substantially in frequency, intensity, and timing among species (Figure 4

and Table S1). Although earlier studies did not report pistil reddening in *S. cortusifolia* var. *cortusifolia* (sect. *Irregulares*) (Shin et al., 2022; Siebold & Zuccarini, 1845; Wakabayashi, 2001), our observations revealed rare and localized reddening during anthesis in this species (Figure 4n and Table S1). This finding suggests that even species lacking conspicuous pistil reddening may express this trait under certain conditions.

Because anthocyanins, commonly involved in floral color change, enhance tolerance to environmental stresses such as strong light, drought, and pathogen attack (Chalker-Scott, 1999; Gould, 2004; Steyn et al., 2002), pistil reddening in *Saxifraga* may have originated or been maintained primarily as a protective response that shields ovules and developing seeds from abiotic stress. Such a preexisting stress-response mechanism could subsequently have been co-opted as a visual signal influencing pollinator visitation when ecological conditions favored this functional shift. In this context, pistil color change in *S. fortunei* may represent a secondary use of a stress-related physiological response.

Within *Saxifraga* sect. *Irregulares*, characterized by zygomorphic flowers, species sharing the distinctive combination observed in *S. fortunei*, namely, patternless white petals and frequent pistil reddening from yellow to red, including *S. rufescens* and *S. serotina*, are likely candidates for similar shifts in pollinator visitation (Balfour, 1916; Pan et al., 2001; Zhang et al., 2020; Zhu et al., 2023; Dey et al., 2025; Table S1). Similar combinations of petal coloration and pistil color change also occur in actinomorphic taxa in other sections, such as *S. mertensiana* (sect. *Heterisia*), and in related genera, including *M. occidentalis* (Watson, 1888; Aiken et al., 2007; Brouillet & Elvander, 2009; Table S1). Because insects have limited spatial resolution, petal spots are thought to contribute more to guiding pollinator behavior at close range than to long-distance attraction (de Ibarra et al., 2015; Rigosi et al., 2017). Given that pistil color change in *S. fortunei* is associated with shifts in visitor behavior at close range within an inflorescence, the presence of prominent petal spots in related species could reduce reliance on pistil-based signaling compared with species lacking such patterning. By contrast, in species such as *S. acerifolia*, which bear only small and inconspicuous petal spots, a similar strategy may be feasible (Wakabayashi, 1973, 2001; Magota et al., 2018; Magota, Sakaguchi, Hirota, et al., 2021; Magota, Sakaguchi, Lee, et al., 2021; Enomoto et al., 2024; Figure 4d,h). Future studies should assess how widespread visitation shifts associated with pistil color change are within sect. *Irregulares*, other sections of *Saxifraga*, and related genera.

5 | CONCLUSION

This study demonstrates that pistil color change in *S. fortunei* is closely associated with pollinator visitation patterns. A rapid transition from yellow to red coincided with strongly reduced visitation to flowers with reddened pistils, while maintaining a conspicuous floral display, thereby potentially enhancing pollination efficiency. Experimental results show that reddening is associated with pollen tubes reaching

the ovules, linking visual signaling with reproductive development. Comparative observations in related taxa suggest that similar systems may be more widespread than previously recognized. These findings expand current understanding of floral color change and highlight the important role of non-perianth floral organs in shaping plant-pollinator interactions.

AUTHOR CONTRIBUTIONS

Kazuma Takizawa and Kenji Suetsugu conceived and designed the study. Kazuma Takizawa and Masayasu Furukawa conducted fieldwork and laboratory experiments. Kazuma Takizawa performed literature review and online database searches. Kazuma Takizawa and Kenji Suetsugu drafted the initial manuscript. All authors revised the manuscript and approved the final version for submission.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Additional supporting information is available online in the Supporting Information.

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