Novel Ideas and Pilot Projects

VISUAL ATTRACTION CUES ASSOCIATED WITH TACHINID POLLINATION: INSIGHTS FROM COLOUR VARIATION IN *SUCCISELLA MICROCEPHALA* (CAPRIFOLIACEAE)

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Abstract—Pollination syndromes describe convergent floral traits linked to specific pollinator groups. While conceptually useful, the application of this framework to diverse insect assemblages, such as Diptera, remains challenging due to their functional heterogeneity. Recent studies have therefore proposed narrowing dipteran pollination into more precise syndromes. In this context, preliminary field observations of flower visitors to *Succisella microcephala* suggest a potential case of specialisation towards tachinid flies. Despite its generalist-like floral morphology, *S. microcephala* exhibits geographic variation in corolla colour and contrasting pigmentation between the corolla tube and lobes. Field observations revealed that populations with darker, more contrasting, flowers were predominantly visited by tachinid flies, which were particularly abundant at higher elevation sites, where *Deschampsia cespitosa*, an important food plant for moth larvae – the main larval hosts of tachinids – was also abundant. These observations suggest a potential adaptive relationship between floral pigmentation and tachinid attraction. Comparative evidence from other European taxa (e.g., *Neotinea ustulata*) further supports the hypothesis of shared, visually mediated traits favouring tachinid attraction and pollination. Additionally, the proximity between flowering and fruiting structures, and the striking resemblance between the dark red immature diaspores of *S. microcephala* and the similarly pigmented globular floral structures in plants associated with tachinid pollination, raise the novel possibility of diaspore-mediated pollinator attraction. Here, we suggest that dark colour structures may be associated with tachinid pollination and tachinid flies may act as potential drivers of an as-yet undescribed pollination syndrome. *Succisella microcephala* represents a promising system to investigate the potential convergence of floral and diaspore traits under pollinator-driven selection and tachinid sensory ecology.

Keywords—Dipsacaceae, generalist and specialist pollination systems, myiophily, pollination biology, Tachinidae

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INTRODUCTION

Pollination syndromes are sets of convergent floral traits thought to have evolved in response to selection imposed by specific groups of pollinators (Fægri & van der Pijl 1979). The classical framework assumes that these trait combinations reflect adaptive specialisation to functionally similar pollinators of one specific taxon, allowing predictions of pollinator identity based on floral phenotype. Recent studies advocate for a more integrative approach that considers pollination syndromes as hypotheses, to be evaluated using empirical data on pollinator effectiveness, trait function, and community context (Dellinger 2020).

While the pollination syndrome framework offers a useful starting point, its application to megadiverse and functionally heterogeneous pollinator groups can be problematic. The recognition of broad categories such as myiophily (i.e., fly pollination), often fails to capture the anatomical, behavioural, physiological and ecological complexity of dipteran pollinators, which encompass more than 70 species-rich families reported as floral visitors (Woodcock et al. 2014). Accurate syndrome predictions in such contexts require the identification of system-specific discriminant traits that relate to the sensory and habitat ecology of the potential pollinators (Dellinger 2020). Early classifications, such as sapromyiophily, described associations with carrion and dung flies attracted to large, dark red flowers mimicking food and oviposition sites (Johnson & Jürgens 2010). Another well-established model involves long-proboscid flies specialised in nectar feeding from flowers with long, narrow corolla tubes in South Africa (Goldblatt & Manning 2000). More recent studies have proposed additional, narrower syndromes within Diptera, including fungus gnat pollination, involving nectar-rewarding dark red flowers that emit acetoin (Mochizuki et al. 2023). Also, tachinid flies (Tachinidae) have been identified as the main pollinators of *Neotinea ustulata* (L.) R.M.Bateman, Pridgeon & M.W.Chase (Orchidaceae), with floral attraction mediated by the dark-coloured inflorescence top (Martel et al., 2021). Nevertheless, our understanding of dipteran pollination remains limited by the fragmentary nature of the available data, particularly in plant clades viewed as generalists, such as Asteraceae or Dipsacoideae (Caprifoliaceae).

Dipsacoids present short tubular, nectar-rewarding flowers that are predominantly protandrous and arranged in involucrate capitula, which provide an effective landing platform for pollinators. Floral colours are most commonly purple, pink, blue, or white (Mayer 2016). In parallel, a wide diversity of pollinator assemblages is observed visiting their inflorescences. In Europe, several species are considered generalists; for example, *Scabiosa columbaria* L. (Müller 1873; Kugler 1955) and *Knautia arvensis* (L.) Coult. (Varga et al. 2022; Franzén & Stenmark 2024; Ollerton et al. 2024) are frequently visited by a broad array of insect guilds, including bees, flies and butterflies. In contrast, *Dipsacus fullonum* L. appears to be primarily pollinated by bumblebees (Müller 1874), whereas pollen-feeding hoverflies (Syrphidae) account for over 60% of flower visitors in *Succisa pratensis* Moench (Hunneman 2003; Štenc et al. 2023). Despite these examples, pollination ecology remains poorly studied across most dipsacoids, and no comprehensive analyses have yet investigated the relationship between specific floral traits and dominant pollinator groups. Notably, preliminary field observations conducted during the ongoing taxonomic revision of *Succisella* Beck in the Iberian Peninsula (Fura et al. 2025) revealed striking variation in floral and diaspore colouration. These colour patterns may reflect adaptations to distinct pollinator guilds, suggesting a promising avenue for future research on trait-mediated pollinator specialisation.

THE INTRIGUING OBSERVATIONS IN *SUCCISELLA MICROCEPHALA* (WILLK.) BECK

Succisella typically exhibit pink, open, short-tubed flowers, arranged in platform-like inflorescences, with easily accessible nectar and pollen rewards, traits that are commonly associated with a generalised pollination system, as observed in other dipsacoids. However, preliminary field observations of *S. microcephala* reveal notable variation in corolla and immature diaspore colouration, as well as distinctive pollinator assemblages, raising questions about the degree of pollinator specialisation in this species, and the potential ecological significance of its floral and diaspore traits.

Succisella microcephala is a Near Threatened species endemic to east-central Portugal and west-central Spain, restricted to temporary wet meadows and ponds, at 250–1495 m a.s.l. (Fura et al. 2025). Fieldwork to characterise its ecology and morphology was carried out at seven locations, representative of the three main distribution centres of its range (Table 1, Fig. 1). At each locality, we recorded corolla and diaspore (i.e., unit consisting of the akene enclosed by the epicalyx, surmounted by the calyx plateau) colour by digital photography. Photographs from four additional localities were obtained from local botanists (Appendix 1). The colour of the tube and lobes of the corolla was annotated separately, and the colour of the epicalyx tube was evaluated in both immature and mature diaspores. Floral visitors were recorded, although not in a standardised manner, since fieldwork was not initially designed to formally evaluate pollinator communities. Each landing of an insect on a flowering capitulum was counted as a visit. Floral visitors were photographed, subsequently

Table 1. Study sites in east-central Portugal and west-central Spain, representative of the three main distribution centres of *Succisella microephala*: the Northern Meseta (sites 1–4), Upper Alberche basin (site 5), and the southern foothills of the Central System in Iberian Peninsula (sites 6–7).

Site code	Site name	Elevation (m a.s.l)	Habitat	Grazing	Observation time
1	Pereruela, Zamora, SP	710	wet meadow with *Juncus effusus* subsp. *effusus*	yes	28-09-2024, 16:35-17:30, GMT+2
2	Martiago, Salamanca, SP	805	wet meadow dominated by *Deschampsia cespitosa* subsp. *cespitosa*	no	28-09-2024, 11:25-12:15, GMT+2
3	Fuentes de Oñoro, Salamanca, SP	735	wet meadow dominated by *Mentha pulegium*	yes	29-09-2024, 16:45-17:15, GMT+2
4	Sabugal-Veiguinha, Beira Alta, PT	820	wet meadow dominated by *Nardus stricta*	yes	30-09-2023, 13:25-16:15, GMT+1
5	Cepeda la Mora, Ávila, SP	1465	wet meadow dominated by *Deschampsia cespitosa* subsp. *caespitosa*, and *Nardus stricta*	no	29-09-2024, 10:10-10:55, GMT+2
6	Velada, Toledo, SP	410	wet meadow dominated by *Molinia caerulea*	no	29-09-2024, 16:30-16:45, GMT+2
7	Candeleda, Ávila, SP	330	wet meadow dominated by *Molinia caerulea*	yes	29-09-2024, 13:50-14:25, GMT+2

identified to the lowest possible taxonomic rank and identifications validated by experts of the different taxonomic groups.

Our field observations put in evidence a previously undocumented pattern of geographically structured variation in corolla colour in *S. microcephala*, in particular, differences in overall corolla colour intensity, and in contrast between the corolla tube and the lobes (Figs. 1, 2), unknown in the other two Iberian species of *Succisella* (Fura et al. 2025). A gradient was observed, from localities presenting corollas with a sharp contrast between the light pink tube and the dark pink abaxial side of the lowermost lobe (Figs. 1C, 2C, 2G-H) to localities presenting less pronounced corolla tube-lobe contrast (white tube and whitish pink to light pink lobes; Fig. 1B). Regardless of these flower colour differences among populations, flower buds are mostly pink to dark pink throughout the range (Fig. 2A), and immature diaspores, occurring simultaneously with flowers and being born on relatively short peduncles, are predominantly dark red (Fig. 2D, I–K), becoming dull brown when mature (Fig. 2E).

Interestingly, the populations seem to have different pollinator assemblages. A total of 40 visits, by 19 species, were recorded in approximately 6 h of observations at six sites (Table 2). Dipterans were the most frequent floral visitors (>60%), followed by lepidopterans (~25%), and hymenopterans (~10%). Among dipterans, tachinids account for over 60% of visits (40% of total visits), standing out as the most frequent, or even exclusive floral visitors, in the three populations of *S. microcephala* with more intensely coloured flowers and presenting a more pronounced corolla tube-lobe contrast (Table 2). Additionally, pollen grains agreeing in size and colour with those of *S. microcephala* were observed on tachinids (Fig. 2F). Butterflies were the only observed flower visitors at two sites, curiously at those with lighter-coloured flowers and less pronounced corolla-lobe contrast (Table 2). Although visited by multiple insect groups, the presence of a broad pollinator assemblage does not preclude the selective influence of a dominant guild, as observed in other generalised systems where trait evolution reflects quantitative variation in pollinator abundance (Gómez et al. 2015a,b).

Succisella microcephala presents floral traits generally associated with a generalised pollination system (i.e., short-tubed corolla, pseudanthia, easily accessible nectar and pollen rewards) and, as such, would be expected to attract a diverse assemblage of floral visitors, with no consistent taxonomic biases. However, our preliminary field

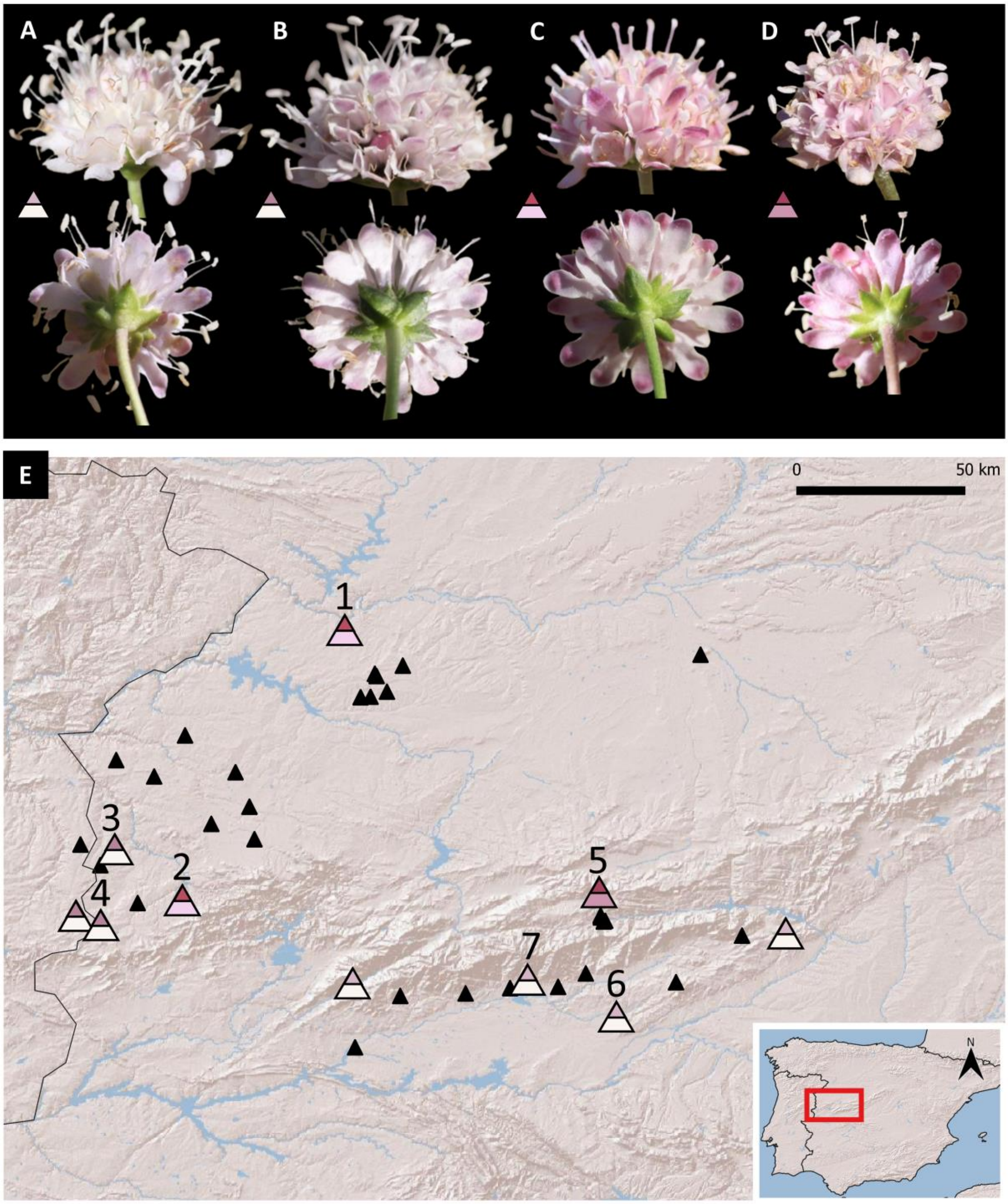

Figure 1. Corolla colour variation in *Succisella microcephala* throughout its range, in east-central Portugal and west-central Spain (A–E). Side and bottom views of flowering capitula: A. Candeleda (site 7). B. Sabugal-Veiguinha (site 4). C. Martiago (site 2). D. Cepeda la Mora (site 5). E. Distribution of *S. microcephala*, following Fura et al. (2025): triangles indicate the occurrence of *S. microcephala* and are colour-coded where information on corolla tube (base) and lobe (apex) colour is available. All sites (1–7) are described in Table 1.

observations reveal a marked predominance of dipteran floral visitors, suggesting a possible affinity with a myiophilous pollination syndrome. The floral morphology partially exhibits several features consistent with this classical syndrome, including relatively shallow corollas, readily accessible nectar rewards and prominently exposed reproductive organs, although the flowers lack perceptible floral scent. However, the pronounced colour contrast between the darker

Table 2. Flower visitors recorded on *Succisella microcephala* at six sites: Pereruela (1), Martiago (2), Cepeda la Mora (5), Fuentes de Oñoro (3), Sabugal-Veiguinha (4), and Candeleda (7).

		Localities					
Visitors	Family	1	2	5	3	4	7
DIPTERA							
Geron sp.	Bombyliidae	1					
Indet.	Calliphoridae					1	
Thecochora cf. *atra*	Conopidae	1					
Neomyia cf. *cornicina*	Muscidae					3	
Merodon cf. *geniculatus*	Syrphidae					1	
Eristalis tenax	Syrphidae	1	1				
cf. *Masicera* sp.	Tachinidae		4				
Peleteria sp.	Tachinidae		2				
Tachina fera/magnicornis	Tachinidae	3					
Siphona sp.	Tachinidae			7			
HYMENOPTERA							
Apis mellifera	Apidae		2				
Heriades sp.	Apidae		1				
Scolia hirta	Scoliidae					1	
LEPIDOPTERA							
Scythris sp.	Scythrididae					1	
Carcharodus alceae	Hesperiidae		1				
Aricia cramera	Lycaenidae	2			3	1	
Lycaena bleusei	Lycaenidae					1	
Argynnis pandora	Nymphalidae						2
Pieris brassicae	Pieridae		1				
Observation time (min.)		55	50	45	35	110	30

corolla lobes and the paler tube diverges from the subdued pigmentation typically described in fly-pollinated flowers (Fægri & van der Pijl 1979), suggesting that the pollination strategy of *S. microcephala* may involve a more complex or specialised interaction than expected under a purely generalised or classical myiophilous framework.

The vivid dark pink to red colouration of the corolla lobes in *S. microcephala* may function as a visual cue involved in a more specialised pollination system than typically observed in other dipsacoids, particularly with respect to the attraction of tachinid flies. This hypothesis is supported by our field observations, which show that tachinid flies (often from multiple species) were the most frequent floral visitors in populations characterised by darker corollas and a pronounced corolla tube-lobe contrast (Fig. 2F –I). Notably, in the population with the most strikingly pigmented flowers, a single morphospecies from the relatively specialised genus *Siphona* Meigen, 1803 was the only visitor recorded. Conversely, tachinids were absent in populations displaying fainter corolla pigmentation and reduced tube-lobe contrast.

The geographically structured variation in corolla colour may thus reflect variable levels of local adaptation towards specialised tachinid pollination. This pattern could be influenced by environmental factors that affect tachinid abundance and community composition, including altitude, vegetation structure, and the availability of host plants required by their parasitoid larvae. For instance, at the highest elevation site (Table 1), only tachinid flies were observed visiting flowers, consistent with the

Figure 2. Flower (A–C, J) and diaspore (D-E, J) development, and tachinid flies as flower visitors (F–I, K) in *Succisella microcephala*. A. Inflorescence in bud. B. Inflorescence in male phase, not fully open. C. Inflorescence in female phase. D. Immature infructescence. E. Mature infructescence (A–E from Martiago). F. *Peleteria* sp. (Martiago, 28.9.2024). G. *Tachina fera/magnicornis* (Pereruela, 28.9.2024). H. Cf. *Masicera* sp. (Martiago, 28.9.2024). I. *Siphona* sp. (Cepeda la Mora, 29.9.2024). J. Inflorescence-infructescence diad. K. Same inflorescence-infructescence with *Runcinia grammica* preying on *Siphona* sp. L. *Cylindromyia* sp. on immature infructescence (Martiago 27.9.2025). Photographs: A, F–I, L by João Farminhão; B by Inês Fura; D, E by Filipe Covelo; J, K by Afonso Petronilho.

broader trend of increased tachinid pollination at higher elevations (Kearns 1992; Martel et al. 2016). Additionally, given that tachinid flies are parasitoids of phytophagous insects, the abundance of suitable lepidopteran larval host species is critical in sustaining local tachinid populations. Several of the observed tachinid taxa, including *Tachina fera/magnicornis*, and representatives of cf. *Masicera*, *Peleteria* Robineau-Desvoidy, 1830, and *Siphona*, are known to parasitise moth larvae, particularly within Noctuidae (Tschorsnig 2017). Interestingly, *Deschampsia cespitosa*, the dominant grass species at sites with the highest tachinid activity, is a documented host for a broad range of noctuid caterpillars (Robinson et al. 2023). This association may indirectly support tachinid abundance and, consequently, influence pollinator assemblages and floral trait evolution in *S. microcephala*.

However, the attraction of tachinid flies might not end in flowering structures. The vivid red colouration of immature infructescences in *S. microcephala* is unique among dipsacoids. Compared to *S. carvalhoana* (Mariz) Baksay and *S. andreae-molinae* Pajarón & Escudero, the other two congeners occurring in the Iberian Peninsula (Fura et al. 2025), *S. microcephala* presents a higher frequency of spatially clustered inflorescence-infructescence diads, in which flowers and diaspores are sometimes juxtaposed (Fig. 2I, J). The overall display likely works as a unit and, to the human eye, is reminiscent of a *N. ustulata* inflorescence, with its 'burnt tip' and open flowers below. Indeed, we observed tachinids (e.g., *Cylindromyia* Meigen 1803, cf. *Masicera* sp., *Siphona* sp.) landing on immature diaspores (Fig. 2L), between visits to inflorescences in flower and bud. Moreover, crab spiders [i.e., *Runcinia grammica* (C. L. Koch, 1837), *Xysticus* sp.] are sometimes observed in immature infructescences, where they spin silk. This is also evidence that immature infructescence have insect activity and serve as hunting ground for typical pollinator predators. Altogether, our preliminary field observations suggest that diaspores may reinforce the attraction of tachinid flies and increase visitation rates of *S. microcephala* inflorescences.

HOW WIDESPREAD IS POLLINATION BY TACHINID FLIES?

With over 8500 described species, all nectar-foraging, distributed in nearly all terrestrial ecosystems, tachinids are important generalist pollinators (Larson et al. 2001; Stireman III 2019). Their setiferous body, like in other 'furry dipterans', facilitates pollen transport without pollen expense to feeding as in bees or hoverflies (Franzén & Larsson 2009). Tachinids are documented as especially important pollinators in highland habitats, where bees become rarer (Kearns 1992; Martel et al. 2016). Yet, little is known about their sensory ecology, but dark red patterns seem to elicit an attraction response (Martel et al. 2019, 2021; Paulus 2022).

In Europe, the food-deceptive *N. ustulata* is the only angiosperm known to rely almost exclusively on tachinids for pollination, although being also regularly visited by other insects (Claessens and Kleynen 2016; Martel et al. 2021; Paulus 2022). It has been experimentally demonstrated that the dark red top of the inflorescence in *N. ustulata* (Fig. 3A) acts as a visual attraction cue to tachinids (Martel et al. 2021; Paulus 2022). Moreover, the production of high concentration of specific floral cuticular alkenes [(Z)-11-C23/C25enes] was shown to be correlated with tachinid pollination (Martel et al. 2021, 2023). Tachinid pollination, mostly by males, occurs in the two phenologically divergent varieties of *N. ustulata*: spring-flowering *N. ustulata* var. *ustulata*, which mostly occurs in dry meadows, is mainly pollinated by *Tachina fera* (Linnaeus, 1761) and *T. magnicornis* (Zetterstedt, 1844), but also by bees (*Anthophora* Latreille, 1803; *Bombus* Latreille, 1802), bibionid flies (*Dilophus* Meigen, 1803), and large dance flies (*Empis tessellata* Fabricius, 1794); while summer-flowering *N. ustulata* var. *aestivalis* (Kümpel) Tali et al., present in both dry and wet meadows, is mostly pollinated by *T. ferox* (Panzer, 1809) and *T. magnicornis*, although bees and beetles were also observed as sporadic pollinators (Claessens and Kleynen 2016; Martel et al. 2021; Paulus 2022).

The same tachinid species that pollinate *N. ustulata* are known to visit other summer-flowering, nectar-rewarding, angiosperms with similar brownish-purple to dark red colour markings and short corolla tubes in Austria, including: *Origanum vulgare* L. (Lamiaceae), in which the dark red calyx contrasts with the pinkish

Figure 3. Overview of confirmed and candidate discriminant traits of tachinid pollination in the European flora: 'dark red beacon' (A–C), and 'pink corolla contrasts' (D–F). A. *Neotinea ustulata* (Orchidaceae), visited by *Tachina magnicornis* (Austria, Hohe Tauern, above the Fusch, 1600 m, 4.7.2006): note the dark top of the inflorescence and the contrast between the white lip and dark pink upper tepals in the open flowers. B. Immature infructescence of *Succisella microcephala* (Caprifoliaceae, Salamanca, Martiago, 28.9.2024): note overall similarity to the dark top in A, and the inflorescence in C. C. *Sanguisorba officinalis* (Rosaceae) visited by the tachinid *Eriothrix rufomaculata* (Czechia, Pavlov, 15.8.2023). D. *Origanum vulgare* (Lamiaceae), visited by *Tachina ferox* (Germany, Neukirchen/Pleiße, 12.7.2023): note colour contrast between bracts and corolla. E. Inflorescence of *Succisella microcephala* (Ávila, Cepeda la Mora, 29.9.2024): note contrast between the corolla tube the abaxial side of the corolla lobe. F. *Eupatorium cannabinum* (Asteraceae) visited by *Siphona* sp. (United Kingdom, Cambridge, Pembroke College, 23.8.2022). Photographs: A. by Hannes F. Paulus, B by Filipe Covelo, C by Pavel Šinkyřík, D by Anonymous, E by João Farminhão, and F by Albert Cardona.

white corolla (Fig. 3D); *Thymus* spp. (Lamiaceae, e.g. *T. pulegioides* L.), also exhibiting a contrast between the dark red calyx and the pink corolla; and *Eupatorium cannabinum* L. (Asteraceae), in which the brownish-purple anthers and involucrate bracts contrast with the remaining pinkish floral parts (Fig. 3F) (Paulus 2022). *Mentha longifolia* (L.) L. (Lamiaceae), also presents a similar contrasting pattern between the typically dark red calyx and the pinkish corolla, and is known to attract tachinids (Kazilas et al. 2020). *Sanguisorba officinalis* L. (Rosaceae), long known to attract dipterans (Kugler 1955), was found to be mainly visited by a diverse assemblage of flies near Bonn, Germany, including sarcophagids and one tachinid species [i.e., *Eriothrix rufomaculata* (De Geer, 1776)] (Abrahamczyk et al. 2023). As a thought experiment, a search for tachinids on iNaturalist (https://www.inaturalist.org/) centred on Czechia and the United Kingdom, revealed multiple interactions between these plant species and tachinids (e.g., Fig. 3C, D, F), including records of tachinids on the dark red inflorescences of *S. officinalis* (Fig. 3C). Interestingly, phenylethylamine was isolated from the flowers of *S. officinalis* (Bunse et al. 2020). Floral amine emission is reported to attract tachinids and other flies and possibly restrict visits by bees (Kugler 1955).

In the neotropics, tachinid pollination by *Eudejeania* Townsend, 1912 and *Peleteria*, is confirmed in the sexual and food-deceptive *Telipogon peruvianus* T.Hashim. (Orchidaceae), an epiphyte from the cloud forests of the west Andes, in which the yellow flower, with a dark red centre, mimics a female tachinid sitting on a yellow Asteracean capitulum, based on visual and chemical cues (Martel et al. 2016, 2019). Some alkanes and alkenes produced by *T. peruvianus* mimic the female sex pheromones of *Eudejeania* (Martel et al. 2019). Tachinid pollination by sexual deception in epiphytic orchids is also suggested in other *Telipogon* Kunth, formerly in *Stellilabium* Schltr., and in *Trichoceros antennifer* (Bonpl.) Kunth (Gasket 2011), all with a dark red centre. In Brazil, a tachinid was found carrying the pollinaria of the forest vine *Gonolobus parviflorus* Decne (Nihei & Schwarz 2011), an asclepidioid with green flowers, although other species of the genus, with unknown pollination biology, present a dark centre (e.g., *G. erianthus* Decne, *G. leotzinii* S.Islas & Quintos-Baez).

From this review of reported cases, only two species, *Neotinea ustulata* and *Telipogon peruvianus*, are confirmed to be predominantly pollinated by tachinid flies (subfamily Tachininae). Striking differences are observed on the level of specialisation among the different systems mentioned here. However, pollination systems are better represented as existing along a continuum between generalisation and specialization rather than as discrete categories (Waser et al. 1996; Armbruster 2017). Populations and species can occupy different positions along this continuum and may shift over time as ecological and selective pressures change. Generalised systems can therefore evolve toward specialisation (or remain generalised) depending on the consistency and strength of selective forces imposed by dominant pollinators and environmental context (Thompson 1994; Armbruster 2017).

ARE TACHINID FLIES ASSOCIATED TO AN UNDESCRIBED POLLINATION SYNDROME?

There are two tantalising parallels, to the human eye, between the floral display of *N. ustulata*, and flower and diaspore colour in *S. microcephala*: (i) the cluster of dark red flowers at the top of the inflorescence in *N. ustulata* (Fig. 3A) is reminiscent of the immature infructescence of *S. microcephala*, presenting diaspores with a dark red tube (Fig. 3B) and of clusters of flower buds of *S. microcephala* (Fig. 2A, B); and (ii) the contrast between the white lip and the upper dark pink tepals of *N. ustulata* flowers is reminiscent of the contrast between the pinkish corolla tube and the pink to dark red abaxial side of the lowermost corolla lobe in populations of *S. microcephala* where tachinids were observed as flower visitors. *Succisella microcephala* exhibits regional variability in key floral traits likely linked with different pollinator assemblages, supporting the idea that it may represent a generalised system under differential selection pressures across environments, potentially evolving in distinct directions along the generalisation–specialisation continuum.

In the Western Palearctic, ecological and chromatic commonalities arise among *Origanum vulgare*, *Thymus pulegioides*, *Eupatorium cannabinum*, *Mentha longifolia*, *Sanguisorba officinalis*, and *S. microcephala*: they are all nectar-rewarding; flower in summer; are frequently visited by tachinids; and exhibit white-light pink-dark pink corolla contrasts (Fig. 3D, E). In the case of *S. officinalis*, the inflorescence colour and shape are reminiscent of the immature infructescence of *S. microcephala*, to the point they were first confused at distance at site 5 (João Farminhão pers. obs.). It is well-known that flowers are more conspicuous than diaspores to pollinators (Renoult et al. 2014). However, if the dark red immature infructescence of *S. microcephala* were analogous to the dark top of *N. ustulata* inflorescences, functioning as an approaching cue to tachinids, this would be the first case of diaspore-mediated pollinator attraction. *Succisella microcephala* presents a very late flowering period, peaking in late September–early October (Fura et al. 2025),

Table 3. Trait synopsis of the two myiophilous syndromes involving dark red displays currently described in the literature, as well as the floral and diaspore traits possibly associated with tachinid pollination.

Predominant insect visitors:	carrion flies	fungus gnats	tachinid flies
Pollination syndrome:	sapromyiophily	nectar-rewarding mycetophily	"*tachinophily*"?
display colour	dark red or brown with purple or reddish blotches	dark red	dark red top or centre, with whitish/pink or yellow contrast
display shape, hairiness, and size	discoid or funnel-shaped, often hairy, large	discoid, glabrous, small	globular or discoid, glabrous or hairy, small
floral scent perception	foul-smelling	buttery, pleasant	faint honey, sweet and slightly peppery, or imperceptible
key floral volatile and cuticular compounds	oligosulphides, phenol, indole, p-cresol	acetoin	tetradecanal, (Z)-11-C23/C25enes
reward	nectar or no reward (food or brood site mimicry)	nectar	nectar or no reward (food and/or sexual mimicry)
flowering time	highly variable	late spring–early summer (Japan, North America)	early summer –early autumn (Europe), year-round (Peruvian Andes)
References	Johnson & Jürgens 2010, and references therein	Mochizuki et al. 2023	Martel et al. 2016, 2019, 2021, 2023; Paulus 2022; this study

when insect activity, namely of bees, has already significantly declined. Selective pressure in plants with synchronous anthesis and fruiting, flowering under scarce pollinator resources, may favour attractive flower buds and immature diaspores, thus, increasing the chance of individual plants being detected by pollinators.

Convergent evolution towards tachinid attraction is a plausible hypothesis to explain the similarities in floral display among *Succisella microcephala*, *Neotinea ustulata* and other late-flowering species with dark red visual cues. Future studies should explore the possibility for a novel pollination syndrome, 'tachinophily', as a means, not a typological end, to speed up research on the pollination biology of these plant species, and the sensory ecology of tachinids. Discriminant traits towards currently described myiophilous syndromes and dark red flowers visited by tachinids are summarised in Table 3. A quantitative assessment of flower and pollinator data is needed to test these hypotheses and formally propose it as a new pollination syndrome. We suggest studies combining standardised visitor censuses, flower (and diaspore in the case of *S. microcephala*) reflectance and headspace gas chromatography, and electrophysiological analyses of tachinids. *Succisella microcephala* represents an excellent system to test the hypotheses proposed here.

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AUTHOR CONTRIBUTION

Concept and design JF & SC, data collection JF, data analysis JF, writing JF & SC, edits and approval for publication JF & SC.

DISCLOSURE STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Please contact the corresponding author for data requests.

APPENDICES

Additional supporting information may be found in the online version of this article:

Figure S1. Additional observations of corolla colour variation in *Succisella microcephala*.

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