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Pollination biology and flower morphology of Austrian Clematis

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Abstract

The genus *Clematis* (Ranunculaceae) is distributed worldwide, and its conspicuous flowers suggest pollination by animals. Four *Clematis* species occur naturally in Austria, representing the three flower types typical for this genus. *C. vitalba* and *C. recta*, with their smaller, white flowers, represent the dish-like flower type, while *C. alpina* represents the bell-shaped type and *C. integrifolia* the tubular type. The latter two species have larger, blue-violet flowers. Although the available research is limited and only a few studies have addressed the pollination biology of *Clematis*, it can be assumed that the morphologically distinct flower types correspond to either a generalist (open, dish-like flowers) or a more specialized (bell-like/tubular flowers) pollination syndrome.

The four *Clematis* species occurring in Austria were studied at three sites in Lower Austria and Styria, with the widespread *C. vitalba* being investigated alongside one additional species at each location. To demonstrate differences in morphology and floral traits, flowers were measured and floral characteristics such as scent and color were documented. Floral rewards (pollen/nectar) were examined, as well the potential for self-pollination. Furthermore, pollinators and visitors were quantitatively recorded and assigned to at least broad groups in order to determine whether the species can be associated with different pollination syndromes. The classification of the four species into generalist and specialized syndromes was supported by the results. *C. vitalba* and *C. recta* with a generalist character were visited by a variety of different pollinators from the orders Diptera, Coleoptera, Hymenoptera, and Lepidoptera. However, only the genus *Bombus* (Hymenoptera) was observed on *C. alpina*. *C. integrifolia* was also visited primarily by larger Hymenoptera, which allows for classification as a more specialized syndrome, although pollination by short-tongued flies and beetles may also be possible at the end of anthesis. All flowers suggest self-pollination at the end of anthesis, offering pollen and nectar as a reward. Nectar was found in all species except *C. recta*, although visits by various Lepidoptera suggest the presence of nectar there as well. Various moths were also observed as pollinators on *C. vitalba* at night. Further investigations into the effectiveness of observed pollinators, the breeding system (outcrossing or selfing) and more precise analyses of floral scents could further refine the picture of the pollination biology of Austrian *Clematis* species.

Zusammenfassung

Die Gattung *Clematis* (Ranunculaceae) ist weltweit verbreitet, und ihre auffälligen Blüten lassen auf eine tierische Bestäubung schließen. Vier *Clematis*-Arten sind in Österreich heimisch und repräsentieren die drei für diese Gattung typischen Blütentypen. *C. vitalba* und *C. recta,* mit ihren kleineren, weißen Blüten gehören zum „schalenförmigen" Blütentyp, während *C. alpina* den „glockenförmigen" und *C. integrifolia* den „röhrenförmigen" Typ repräsentiert. Die beiden letztgenannten Arten besitzen größere, blau-violette Blüten. Obwohl es derzeit nur wenige Studien zur Bestäubungsbiologie von *Clematis* gibt, kann angenommen werden, dass die morphologisch unterschiedlichen Blüten einem generalistischen- (offene, schalenförmige Blüten) oder einem spezialisierten (glockenförmige/röhrenförmige Blüten) Bestäubungssyndrom zugeordnet werden können. Die Bestäubungsbiologie der vier in Österreich vorkommenden Arten wurde in drei Gebieten in Niederösterreich und der Steiermark untersucht, wobei die weit verbreitete *C. vitalba* an jedem der drei Standorte parallel zu einer der anderen dort vorkommenden Arten untersucht wurde. Um Unterschiede in Morphologie und Blütenmerkmalen aufzuzeigen, wurden die Blüten vermessen und Merkmale wie Duft und Farbe dokumentiert. Die Belohnungen (Pollen/Nektar), sowie die Möglichkeit der Selbstbestäubung wurden untersucht. Darüber hinaus wurden Bestäuber und Besucher quantitativ erfasst und (zumindest grob) Gruppen zugeordnet, um festzustellen, ob die Arten mit verschiedenen Bestäubungssyndromen assoziiert werden können. Die Einteilung der vier Arten in generalistische und stärker spezialisierte Syndrome konnte bestätigt werden. *C. vitalba* und *C. recta* mit generalistischem Charakter wurden von einer Vielzahl verschiedener Bestäuber aus den Ordnungen Diptera, Coleoptera, Hymenoptera und Lepidoptera besucht. Auf *C. alpina* wurde jedoch nur die Gattung *Bombus* (Hymenoptera) beobachtet. *C. integrifolia* wurde ebenfalls hauptsächlich von größeren Hautflüglern besucht, was eine Klassifizierung als stärker spezialisiertes Syndrom erlaubt, obwohl eine Bestäubung durch Fliegen und Käfer am Ende der Anthese bei *C. integrifolia* ebenfalls möglich sein könnte. Alle Blüten deuten auf Selbstbestäubung am Ende der Blütezeit hin, wobei Pollen und Nektar als Belohnung angeboten werden. Nur bei *C. recta* konnte kein Nektar gefunden werden, obwohl Besuche verschiedener Schmetterlinge auf das Vorhandensein von Nektar auch dort schließen lassen. Verschiedene Nachtfalter wurden zudem nachts als Bestäuber an *C. vitalba* beobachtet. Weitere Untersuchungen sind erforderlich, um die effektiven Bestäuber der österreichischen *Clematis* zu ermitteln, sowie Untersuchungen zum Fortpflanzungssystem (Selbstbestäubung) und präzisere Analysen der Blütendüfte, welche das Bild der Bestäubungsbiologie der österreichischen *Clematis* Arten weiter verfeinern würden.

Table of content

Introduction

With their great morphological diversity, angiosperms are the most diverse group of plants in terms of form and species, with the flower being the characteristic that distinguishes them from all other plant groups (Raven et al., 1985). In angiosperm flowers, the perianth - petals and sepals - encloses the reproductive organs, where male and female structures are typically combined in a hermaphroditic flower (Willmer, 2011). The male androecium is formed from the pollen-producing stamens, which in turn enclose the gynoecium. It consists of the pollen-receiving stigma, style, and ovary, which together form the female reproductive organ (Rudall, 2007). For successful reproduction, i.e., the transfer of male pollen grains to a receptive female stigma, plants utilize pollination vectors. These vectors can be either biotic (animals) or abiotic (e.g., wind) (Faegri & van der Pijl, 1979), with the majority of angiosperms (approximately 85%) relying on animal pollination (Ollerton et al., 2011).

Pollinators are attracted to flowers through colorful displays or abundant nectar and pollen rewards, with frequent visitation aimed at achieving as much outcross pollen transfer as possible (Raven et al. 1985). Nevertheless, many species possess mixed reproductive systems that allow for autonomous selfing in addition to animal-mediated pollination (Ollerton et al., 2011). In a flower that combines male and female reproductive organs, selfing seems obvious, but the strategy of cross-pollination has become established, most likely due to the advantage of parental gene combination and to avoid inbreeding depression, which ensures higher fitness in offspring (Charlesworth & Willis, 2009). Despite this, hermaphroditic flowers are widespread (Barett & Hough, 2013) and angiosperms have developed various strategies to prevent self-pollination, including temporal (protandry or protogyny) and spatial (herkogamy) separation of the stigma and anthers (Lloyd & Webb, 1986). To achieve advantageous cross-pollination, plants use attractants that appeal to the potential pollinators' feeding, sexual, or breeding instincts. The urge to feed is the reason for most visits to flowers, and plants offer food mainly in the form of sugary nectar or pollen (Willmer, 2011).

The various floral characteristics of angiosperms are likely the result of selection and can increase the plant's reproductive success (Schiestl & Johnson, 2013). Characteristics such as color, scent, or shape can in combination or individually affect the attraction of animal intermediaries, in order to transfer the male gametes (Faegri & van der Pijl, 1979; Willmer, 2011). Once an animal visits the flower of a plant species and transfers pollen to a receptive stigma, it can be classified as a pollinator. This relationship between plants and animals can vary from generalized to highly specialized (Faegri & Van der Pijl, 1979; Ollerton et al., 2007). Generalization and specialization in pollination systems can be defined along different axes, e.g. ecological (number of interacting pollinator species) or functional (effective pollinators)

generalization/specialization (Ollerton et al., 2007). Generalist flowers interact with a wide range of pollinators, although they may differ in effectiveness (Waser et al., 1996; Ollerton et al., 2007). In contrast specialized flowers are typically adapted to a smaller range of pollinators or a specific functional group, which is often the result of pollinator-mediated selection on floral traits (Fenster et al., 2004).

A central concept in pollination biology, which examines plant–pollinator interactions, is that of pollination syndromes. Building on the early work of Delpino (1873–1874), this concept proposes that specific combinations of floral traits are correlated with particular groups of pollinators, reflecting adaptations to pollinators that transfer pollen most effectively (Stebbins, 1970; Faegri & van der Pijl, 1979). Specialized functional pollinator groups form units that prefer the same combination of flower characteristics (Fenster et al., 2004) and thus, it is assumed that certain floral syndromes can predict efficient pollinators that are likely to occur on the flowers of a given plant (Faegri & van der Pijl, 1979). Since the late 20th century, the universality of pollination syndromes has been increasingly questioned. While classical theory assumes relatively specialized relationships between plants and their pollinators, empirical studies have demonstrated that many plant species have a broad range of pollinators, indicating that generalization is more common than predicted by classical syndrome theory (Waser et al., 1996; Ollerton et al., 2009). Current perspectives show that pollination syndromes can be a useful model but should not oversimplify a complex system. Instead, their interpretation should always be context-dependent, taking into account ecological factors such as pollinator availability and environmental conditions (Ollerton et al., 2007; Dellinger, 2020).

In a recent study, Temeles and Dalsgaard (2026) highlight that pollinator-competition has been overlooked in previous research on pollination syndromes. They suggest that competition can promote specialization and cause differences in floral traits when floral morphology alone does not predict interactions. However, other studies demonstrate that floral traits can have predictive value, especially for identifying effective pollinators rather than the full spectrum of floral visitors (Fenster et al.; 2004; Rosas-Guerrero et al., 2014; Dellinger, 2020). Key floral traits considered in the study of pollination syndromes include flower morphology (shape and size), color, scent, reward type (nectar and/or pollen) and accessibility, position of sexual organs, as well as phenology, which influence the attraction of pollinators and their efficiency in pollen transfer (Faegri and van der Pijl, 1979; Fenster et al.; 2004; Rosas-Guerrero, 2014).

Clematis L. (Ranunculaceae) is a cosmopolitan genus and includes about 300 species (Wang & Bartholomew, 2001). A majority of species exhibit characteristics of woody vines, a smaller percentage are perennial herbaceous plants, subshrubs or shrubs, with typically terminal inflorescences that range from solitary flowers up to branched inflorescences with a

large number of flowers (Wang & Li, 2005). *Clematis* spp. often have showy corollas, with typically 4-5 sepals (petals absent) (Wang & Bartholomew, 2001) in different forms and shapes, which suggest the attraction of different animals for pollination. Diverse shapes of *Clematis* flowers can be classified in three different types: dish-like type with spreading sepals, bell-like type with ascending sepals and the tubular type with erect sepals (Fig. 1) (Wang & Li 2004; Jiang et al., 2010). There are four species of *Clematis* occurring in Austria, *C. vitalba* L., *C. recta* L., *C. alpina* (L.) Mill. and *C. integrifolia* L. (Fischer et al., 2008). The four species represent the three floral types, with *C. vitalba* and *C. recta* representing the dish-like -, *C. alpina* the bell-shaped -, and *C. integrifolia* the tubular type.

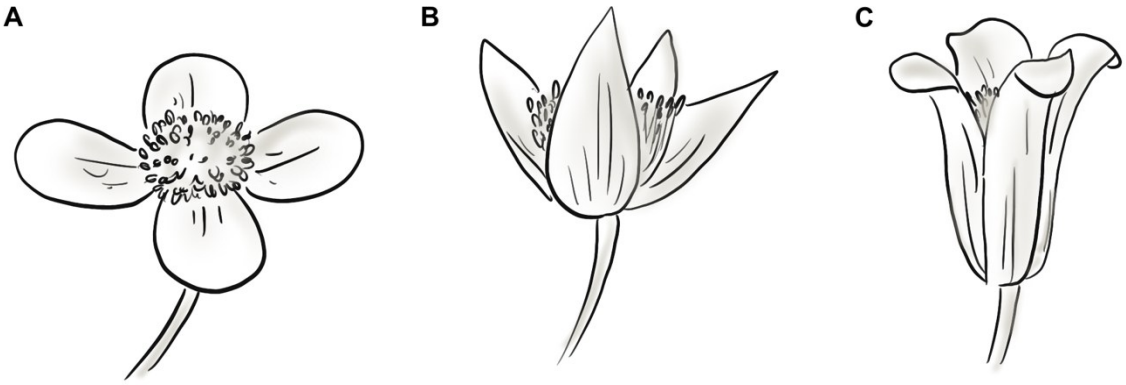


Fig. 1: Types of *Clematis* flowers: A: dish-like type, B: bell-like type and C: tubular type (Fig. adapted, based on Wang & Li, 2004)

Studies about the pollination biology of *Clematis* have been rare overall and there are no detailed observations on the pollination biology of the *Clematis* species occurring in Austria. There is some data on pollinators from Knuth (1898) from northern Germany, who compiled various observations of flower visitors to *Clematis* species, including those found in Austria. For the dish-shaped *C. vitalba*, Knuth (1898) primarily reports various Diptera (Muscidae and Syrphidae) as well as a range of Hymenoptera, particularly wild bees, but also *Apis mellifera* and members of the Vespidae. Similarly, *C. recta*, which exhibits comparable floral morphology, is visited by a largely overlapping assemblage of pollinators; however, Coleoptera (Scarabeidae) have additionally been reported on its flowers. In contrast various Apidae species were observed visiting the bell-shaped *C. alpina*, while no pollinator data are available for *C. integrifolia*.

Of particular interest for this study is a paper by Jiang et al. (2010), that comparatively examined the pollination and reproductive biology of three *Clematis* species occurring in China, representing all three floral types of *Clematis*. The study aimed to contribute to the

understanding of pollination syndromes and reproductive characteristics of the genus. The floral morphology of the dish-shaped *Clematis chrysocoma* is similar to that of the Austrian species *C. vitalba* and *C. recta*. In contrast, the bell-shaped flowers of *C. akebioides* are comparable to those of *C. alpina*, while the tubular flowers of *C. rhederiana* show similarities to *C. integrifolia*. Jiang et al. (2010) showed that generalized flowers with dish-like shapes are mainly pollinated by insects like flies, whereas flowers with tubular and bell-like shapes are specialized on long tongued insects like bumblebees. Due to its comparability with Austrian *Clematis* species, this study provides a basis for drawing comparisons and making predictions about the pollinators and reproductive biology of Austrian species.

In another study Tomas et al. (2022) examined two Mediterranean *Clematis* species, *C. flammula*, with dish-like flowers, and *C. cirrhosa*, with bell-like flowers, which bloom in different seasons and thus provide an important food source for insects throughout the year. The species with dish-like flowers was visited by different pollinator species (primarily various Hymenoptera and Diptera, especially Syrphidae), while the bell-like flowers were visited almost exclusively by Hymenoptera (*A. mellifera* and *B. terrestris*).

Some other studies focusing primarily on individual *Clematis* species and specific aspects of the reproductive biology. There are two studies from Japan by Dohzono & Suzuki (2002) and Dohzono et al. (2004), who examined *C. stans*, a species with pendant, tubular flowers (similar to *C. integrifolia*), which shows a change in calyx tube length during its flowering period, being pollinated primarily by a long-tongued bumblebee species at the beginning (longer tube) and by a short-tongued bumblebee species towards the end (shorter tube) of anthesis. These studies demonstrate an example of a specialized system, where the tube length is correlated with the proboscis length of the pollinators (Nilsson, 1988). The temporal change in the calyx tube length of *C. stans* enables the attraction of two different pollinators and thereby increasing pollination success and reproductive output (Dohzono & Suzuki, 2002; Dohzono et al., 2004). Borkent and Harder (2006) investigated the dioecious *C. ligusticifolia* (flowers similar to *C. vitalba* and *C. recta*) in Canada and showed that generalist flies are their main pollinator, which visit both female and male flowers equally and, despite limited specialization, act as effective pollen vectors. Another study by Redmond & Stout (2018) examined the reproductive biology and pollinators of *C. vitalba*, which is classified as an invasive species in Ireland. They demonstrated that the plant is capable of both sexual and uniparental reproduction and is pollinated by a wide variety of insects, particularly hoverflies.

The studies cited above, which also investigated aspects of the reproductive system (Knuth, 1898; Jiang et al., 2010; Redmond & Stout; 2018 & Tomas et al., 2022), indicate that *Clematis* species with hermaphroditic flowers are generally capable of both self- and cross-pollination. However, seed production is reduced in self-pollinated flowers, compared to natural pollinated flowers (Jiang et al., 2010; Redmond & Stout; 2018 & Tomas et al., 2022). Knuth

(1898) describes that, in all four species occurring in Austria, anther dehiscence begins at the periphery of the flower and gradually progresses inward toward the centrally positioned stigmas, thereby facilitating self-pollination towards the end of anthesis. A similar pattern was observed by Jiang et al. (2010) in two of the three species studied; however, in the bell-shaped *C. rhederiana*, anther dehiscence proceeds in the opposite direction, from the center outward.

The Austrian *Clematis* species show conspicuous flowers with medium-sized to large corollas, suggesting the attraction of insects for pollination. Based on the studies mentioned above, the three floral types represented among these species (dish-like, bell-like, and tubular) suggest that specific floral traits are associated with distinct pollinator groups. Species with a dish-shaped flowers typically exhibit a generalist pollination system, attracting a wider range of pollinators, particularly various flies, hymenopterans, and beetles. In contrast, pendant, bell-shaped or tubular flowers appear to be more specialized, showing adaption to long-tongued insects, primarily within the Hymenoptera.

This Master thesis aims to provide an overview of the pollination biology and flower morphology of Austrian *Clematis* species. I want to answer the following questions about flower morphology and flower traits: (1) How do the four *Clematis* species differ morphologically? (2) Which reward do they offer (pollen/nectar)? (3) Is there the potential for self-pollination and (4) Do floral traits reflect adaptations to distinct pollinator groups? Because the four species differ in floral color (white and blue) and corolla shape (upright and open flowers versus pendant and bell-shaped flowers), I expect to find different assemblages of pollinator species. Based on the studies mentioned above, I hypothesize that *C. vitalba* and *C. recta* belong to a generalist pollination syndrome, attracting various insects as pollinators, whereas *C. alpina* and *C. integrifolia* are more specialized and adapted to pollination by long-tongued insects, particularly bumblebees. I hypothesize that the apparent differences in flower morphology among the four species – particularly between the dish-shaped (*C. vitalba* and *C. recta*) and the bell-shaped/tubular (*C. alpina* and *C. integrifolia*) species – are reflected in measurable variation in floral traits, with characteristics matching their suggested syndromes (e.g. more nectar for bee pollinated species). Additionally, I expect all species to show some capacity for self-pollination towards the end of anthesis. If pollination syndromes proposed by Jiang et al. (2010) are not applicable to European *Clematis*, I could expect that co-occurring species (*C. vitalba* with all other species) share more similar pollinator communities - reflecting local pollinator availability - than geographically separated populations of the same species (*C. vitalba*). Further I hypothesize that nocturnal visitors differ from typical daytime pollinators, found on the flowers of *C. vitalba* and *C. recta*.

Material & Methods

Study species

This study investigated the four *Clematis* species occurring in Austria. *Clematis vitalba* is a cosmopolitan species, growing as a woody liana with erect, spreading flowers arranged in umbrella panicles, white disc-shaped perianth and a flowering period from June to July (October). It is common in all Austrian states in colline to montane regions and widespread across Europe and Northern Africa and considered as invasive in North America and New Zealand. It is a pioneer plant that occurs in fresh to moist, sparse deciduous forests and shrubs, especially in alluvial forests and forest edges (Fig. 2, A and B). *Clematis recta* is herbaceous, with erect, terminal flowers similar in color and shape to *C. vitalba,* and flowers during June (July). It grows in colline to submontane, summer-warm sites such as vineyard edges and forest clearings in Eastern and Southern Europe and is relatively rare in the Pannonian region of Austria (Fig. 2, C and D). *Clematis alpina* is a climbing shrub with bell-shaped flowers and blue to purple perianth, with a flowering period between May and July. It occurs scattered in lower montane to subalpine forests on calcareous soils (Fig. 3, C and D), but also on siliceous bedrock in the Central Alps (e.g., Tyrol). *Clematis integrifolia* is an herb with single, nodding to pendant tubular flowers with purple perianth and a flowering period from May to June (October). It is rare in Austria and occurs only in the alluvial meadows of the Morava River in the Pannonian region of Eastern Austria (Fig. 3, A and B). All information on the species' distributions comes from Fischer et al., 2008. Petals in the family of Ranunculaceae only occur ancestrally (Delpeuch et al., 2022), the conspicuous part of *Clematis* flowers is formed by the sepals (Knuth, 1898); therefore, in the following the terms "sepals" and "calyx" will be used.

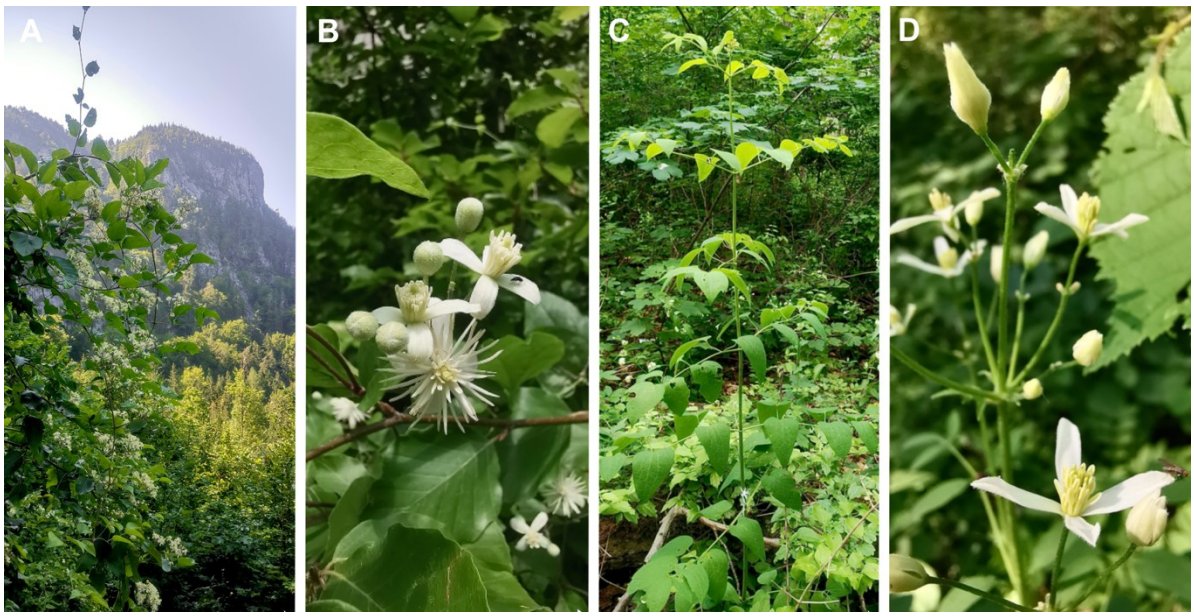


Fig. 2: Growth habit and flowers of the studied species *C. vitalba* (A and B) and *C. recta* (C and D) with their white, disc-shaped perianth

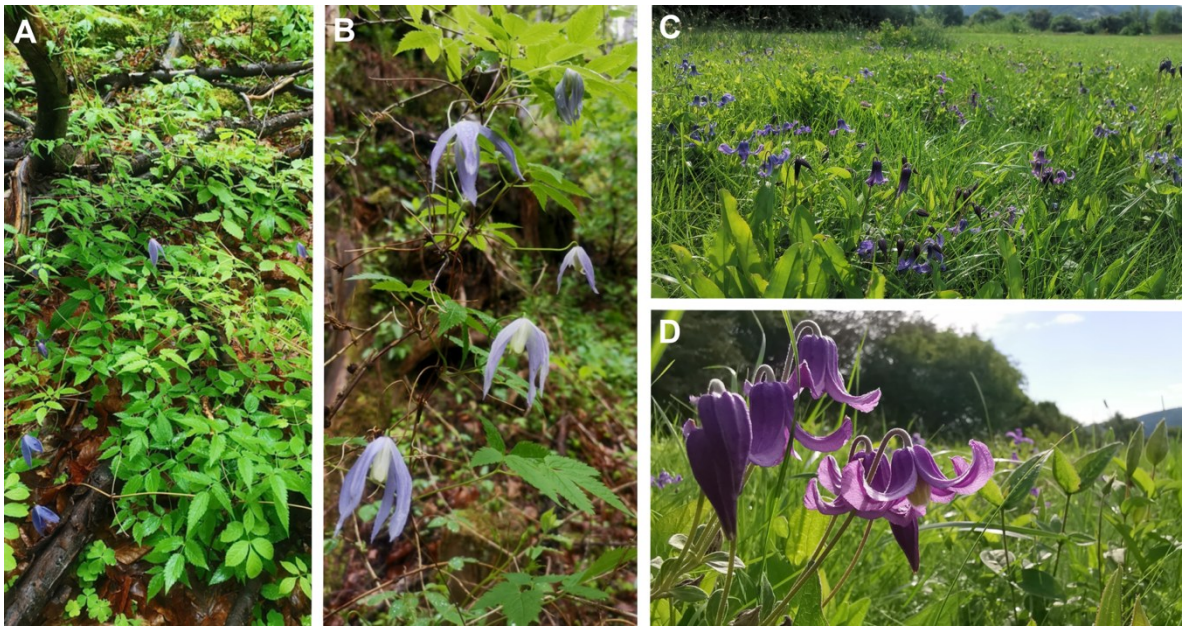


Fig. 3: Growth habit and flowers of the studied species *C. alpina* (A, B) and *C. integrifolia* (C, D) with bell-shaped flowers and blue-violet perianth

Study sites and period

Fieldwork was conducted from May to August 2021 at different sites in Austria. Data for *C. alpina* were collected in Mixnitz (Styria) near Bärenschützklamm (47.336406, 15.386157) on 20, 21, 28 and 29 May. Data for *C. recta* were collected in Gumpoldskirchen (48.052156, 16.277646) and Pfaffstätten (48.0312821, 16.2532784), in Lower Austria, on 07, 08, 15, 16 and 17 June and in Schloßhof (48.2118352, 16.9583842), the site where *C. integrifolia* co-occurred, on 22 June. Data for *C. integrifolia* were collected in Schloßhof (Lower Austria) on 22, 24, 30 June and 09 and 11 August. *Clematis vitalba* was studied at all of the above-mentioned locations on 23 and 24 June (Bärenschützklamm), 28 and 29 June (Gumpoldskirchen) and 12 and 13 August (Schloßhof and Marchegg, close to Schloßhof (48.2472742, 16.9237328)). Gumpoldskirchen/Pfaffstätten, the study area for *C. recta,* lies on the thermal region, which was characterized by a dry climate, thermophilic tree species (such as pine and downy oak forests) and dry grassland fragments, with *C. recta* growing in the open or light marginal area of the forests. The habitat of *C. alpina* in the Bärenschützklamm was characterized by beech and spruce forests of low to intermediate density surrounded by limestone cliffs, where the species occurs sporadically in the undergrowth. *C. integrifolia* was found in a wet meadow at the edge of the forest in the floodplains of the Morava River. *C. vitalba* was found at all the above-mentioned locations, growing in Schloßhof on the nearby, drier dam and in Marchegg at the edge of the alluvial forest (Tab. 1).

At each collection site, 13 to 23 individuals were selected, depending on availability of suitable plants. Every individual was marked and given an ID with a serial number.

Tab. 1: Locations and periods of data collection of *C. alpina*, *C. recta*, *C. integrifolia* and *C. vitalba*

Species	***Individuals studied***	***Location***	***Dates***
C. alpina	*n* = 30	Bärenschützklamm, Styria	20, 21, 28, 29 May
C. recta	*n* = 30	Gumpoldskirchen, Lower Austria	07, 15, 16 June
		Pfaffstätten, Lower Austria	08, 17 June
		Schloßhof, Lower Austria	22 June
C. integrifolia	*n* = 30	Schloßhof, Lower Austria	22, 24, 30 June
			09, 11 August
C. vitalba	*n* = 30	Bärenschützklamm, Styria	23, 24 June
		Gumpoldskirchen, Lower Austria	28, 29 June
		Schloßhof / Marchegg, Lower Austria	12, 13 August

Floral morphology

For the investigations of floral morphology and differences between the Austrian *Clematis* species, 30 flowers of each species were randomly collected and measured. The following floral characters were recorded (Tab. 2): floral color and odor strength, nectar quantity (µl), sepal size (length, mm), calyx opening (mm), calyx diameter (mm, Fig. 4), length of staminodes (if present, mm), length of stamens (mm) and length of gynoecium (mm), number of stamens and pistils and stigma receptivity. The tested stigmas were chosen randomly out of the measured flowers and receptivity was tested on up to 25 stigmas of each species. Floral color was scored by eye and floral odor strength was determined by directly smelling the flowers by nose (slight, medium, strong). Nectar was extracted with 2µl capillary tubes (Hirschmann) and measured with a pocket refractometer (Bellingham+Stanley) for sugar concentrations from 0-50%. Sepal size, calyx opening and diameter and maximum lengths of staminodes, gynoecium and androecium were measured with a digital caliper. To measure the flower organs and test the receptivity of stigmas, the flowers were dissected carefully to separate the staminodes and gynoecium. The androecium and gynoecium length were measured first, then the stigma receptivity was tested and finally stamens and pistils were counted. To test for stigma receptivity, MQuant™ Peroxide Test (0.5-25 mg/l H_2O_2) was used. The stigma was dipped in distilled water and then wiped on the test strip. A color scale from colorless (not receptive) to light to strong blue (receptive) then indicated receptivity of the stigmas.

Depending on the number of closed/opened stamens counted upon floral dissection, flowers were categorized as “young” (predominantly closed stamens) or “old” flowers (predominantly opened stamens). Pistils were collected from up to 12 flowers to examine the presence of pollen on young and old flowers with scanning electron microscopy (SEM). For

each of the four species, a pistil from a young an old flower was prepared for SEM analysis. The samples were dehydrated with ethanol (first 70%, 85%, then 96%), critical point dried with CP Autosamdri-815, and then coated with gold (sputter coater SCD 050). Mounted in a sample holder, the pistils could be examined for the presence pollen grains using the JOEL JSM-6390.

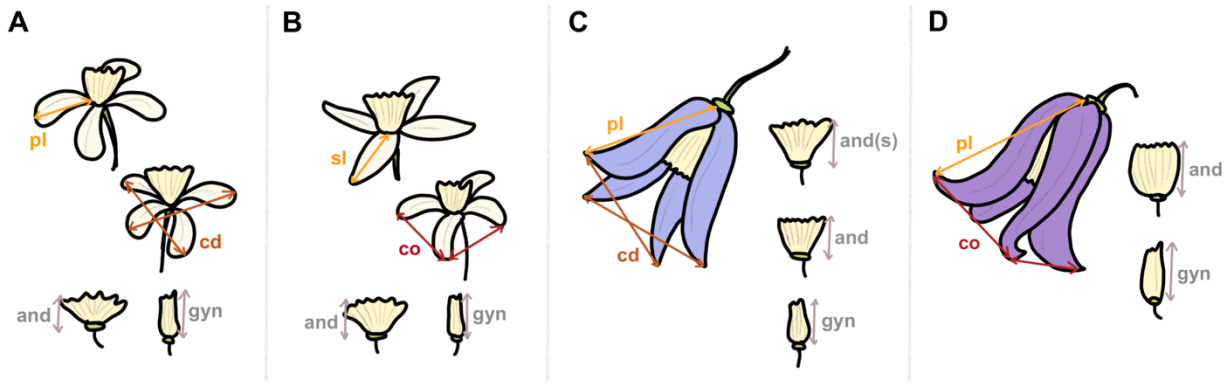


Fig. 4: Measurements made at *C. alpina* (A), *C. integrifolia* (B), *C. vitalba* (C) and *C. recta* (D) flowers: sepal length (pl), calyx diameter (cd), calyx opening (co), sterile androecium (staminodes) length (and(s)), fertile androecium length (and) and gynoecium length (gyn)

To show the differences in floral measurements (sepal length, calyx opening calyx diameter, length of staminodes, stamens and gynoecium), bar plots were created using Microsoft Excel (Version 16.77.1). Further RStudio (version 2024.12.1+563) was used to compare the floral morphology among the four *Clematis* species. A nonmetric multidimensional scaling (NMDS), using function metaMDS(), was used to visualize the differences in floral traits (sepal length, calyx opening calyx diameter, length of staminodes, stamens and gynoecium, number of stamens and pistils) between species. Functions adonis2() and pairwise.adonis() from package 'vegan' (Oksanen et al., 2025) and 'pairwiseAdonis' (Martinez, 2017) were used to show significant differences in floral traits. The same procedure was repeated to compare floral morphology of *C. vitalba* in different localities (Bärenschützklamm, Gumpoldskirchen and Schloßhof/Marchegg).

Pollination biology

Studies on floral pollinators and visitors were conducted throughout the day between 8:25am at the earliest and 5:40pm at the latest. Observations were made in intervals of 30 minutes on the plants marked at the beginning. Since the number of flowers varies greatly from species to species (from one flower per individual in *C. alpina* and *C. integrifolia* to hundreds per individual in *C. vitalba*), observations were made on either more neighboring patches (individuals) with a small number of flowers at the same time (*C. alpina*) or on a single individual with several flowers. The number of watched flowers per observation round was noted and estimated for *C. vitalba* and partially *C. recta*, as these can be very rich in flowers. Time, details

about the weather (temperature, wind, cloud cover) and pollinators/visitors were recorded. Observation was done from a distance of approximately 0.5-1m. Insects that clearly interacted with reproductive organs (stamens and/or stigmas), technically allowing for transfer of pollen grains, were classified as pollinators, all other insects were classified as visitors. Morphospecies (e.g. bumblebee, syrphid fly...) of insects were noted and if possible, a photo was taken for more precise identification. This was done instead of collecting insects, as catching during the observation period took too much time and the identification from photographs at coarser taxonomic resolutions was sufficient for the purposes of the study (i.e., documenting pollination syndromes rather than detailed pollinator taxonomic diversity). When possible, the number of flower visits (potential pollination events) of each pollinator was also documented. In the case of *Apis mellifera* on *C. vitalba* at Bärenschützklamm, an average of 10 flower visits was determined, as the large quantity of individuals made it impossible to count visits of each individual.

In addition to diurnal pollinator observations, observations at night were made on *C. recta* (16 June 2021) and *C. vitalba* (17 August 2021) to check if there are nocturnal pollinators. From dusk (9pm) onwards, three observation rounds were made (approximately every hour) where all plants were checked for the presence of nocturnal pollinators. When animals were encountered on the flowers, their morphospecies was noted and, if possible, a photo was taken for identification.

The pollinator visitation rate (visits per flower per hour) was calculated by dividing the number of flower visits by pollinators (potential pollination events) by the number of flowers (in the observed patch) and then multiplying by two (to get at the VR per hour). To show differences in absolute numbers of pollinators and visitation rates among species, tables and pie charts including all pollinator species were created using Microsoft Excel. Further, RStudio (version 2024.12.1+563) was used to test for significant distances in pollinator composition (visitation rates) between species using functions adonis2() (package ‘vegan’) and pairwise.adonis() (package ‘pairwiseAdonis’). Principal Component Analysis (PCA) was used to visualize data but due to the low explanatory power of the PCA, likely driven by the low number of species with high visitation rates, bar plots were created using the function ggplot2() to visualize differences between the four *Clematis* species, and also *C. vitalba* separately at the different observation sites. Visitation rates of observed pollinators were calculated for each *Clematis* species. To test for differences in visitation rates among species, a Kruskal-Wallis test was made, using the function kruskal.test() in R.

Results

Floral traits

The smaller, whitish, disc-shaped flowers of *C. vitalba* and *C. recta* (Fig. 6) differ clearly from the larger bluish, bell-shaped flowers of *C. alpina* and *C. integrifolia* (Fig. 7). In all species, anther dehiscence occurred from the outside of the androecium to the inside (floral center). Peroxide tests showed that stigmas were already receptive from the opening of the flower onwards, and stigmas were receptive in both flowers considered “young” and “old”. *C. recta* was the only species where no nectar production could be found in the observed flowers. In all other *Clematis* species, nectar is secreted at the inner basal part of the fertile stamens and in *C. alpina*, the carpels are additionally enclosed by sterile spathulate staminodes (Li et al., 2021) (Fig. 8). All four species emitted a scent that could be detected in the field by directly smelling them by nose. It ranged from slight to strong. In *C. vitalba*, the odor of a majority of flowers was intermediate (*n* = 15), followed by strong (*n* = 10) and slight scent (*n* = 5). Flowers of *C. recta* also emitted mostly intermediately strong scent (*n* = 16), followed by slightly (*n* = 10) and strongly scented flowers (*n* = 4). In *C. alpina,* most flowers smelled slightly (*n* = 20), there was an equal number of intermediately and strongly smelling flowers (*n* = 5). In the case of *C. integrifolia*, the majority had an intermediate scent (*n* = 18), the rest had slight and strong scents (n = 6 each) (Fig. 9).

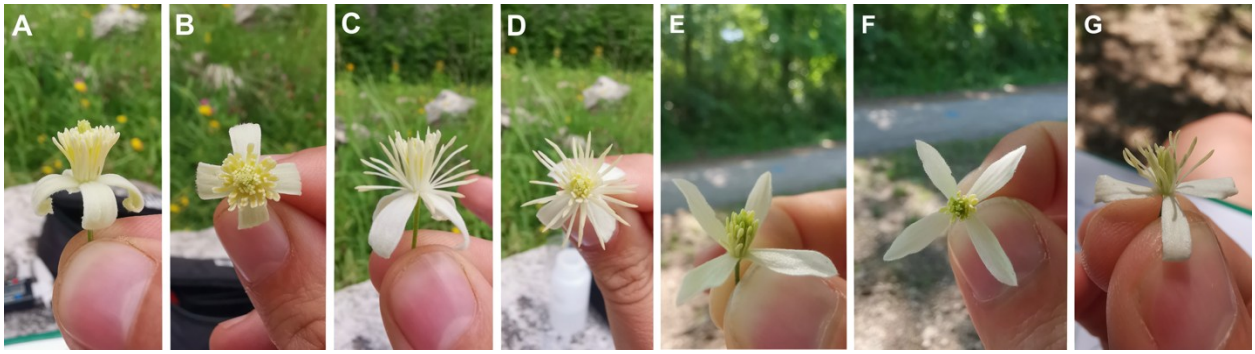


Fig. 6: Disc-shaped flowers of *C. vitalba* (**A - D**) and *C. recta* (**E - G**), **A/B** and **E/F** represent young flowers with predominance of closed (pre-anthetic) stamens aggregated in the flora center, **C/D** and **G** represent older flowers with predominance of open (anthetic) stamens that spread out more.

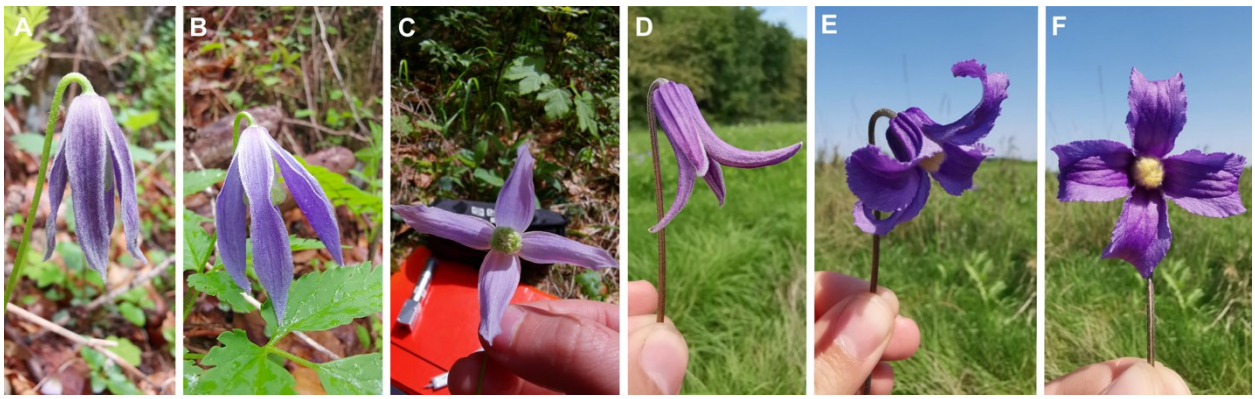


Fig. 7: Bell-shaped flowers of *C. alpina* (**A - C**) and *C. integrifolia* (**D - F**), **A** and **D** show young flowers that have not yet fully opened, **B** and **E** shows older flowers with spread-out calyces.

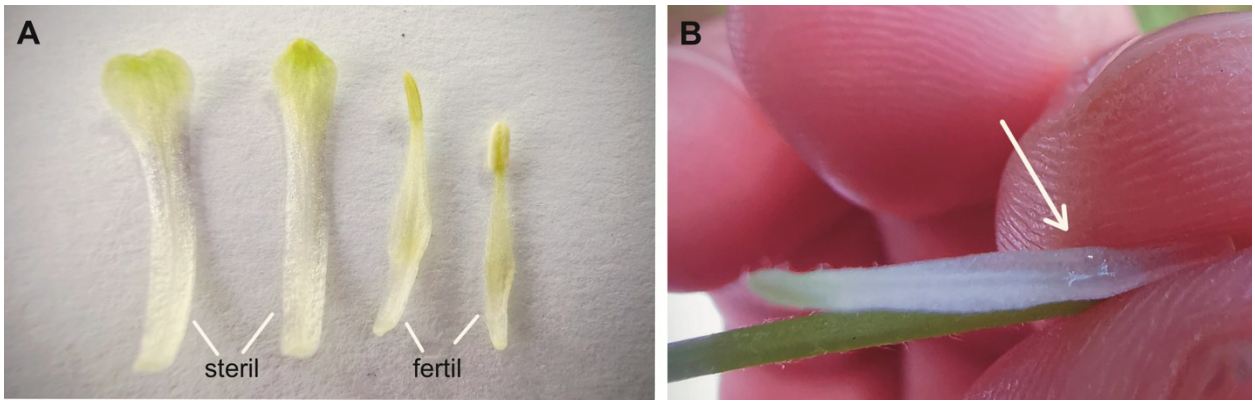


Fig. 8: A: Sterile spathulate staminodes, located on the outside of the androecium, covering the fertile stamen in the center; together, they form the androecium of *C. alpina.* **B**: the site of nectar secretion on the basal inner side of the stamens, a stamen of *C. alpina* is shown.

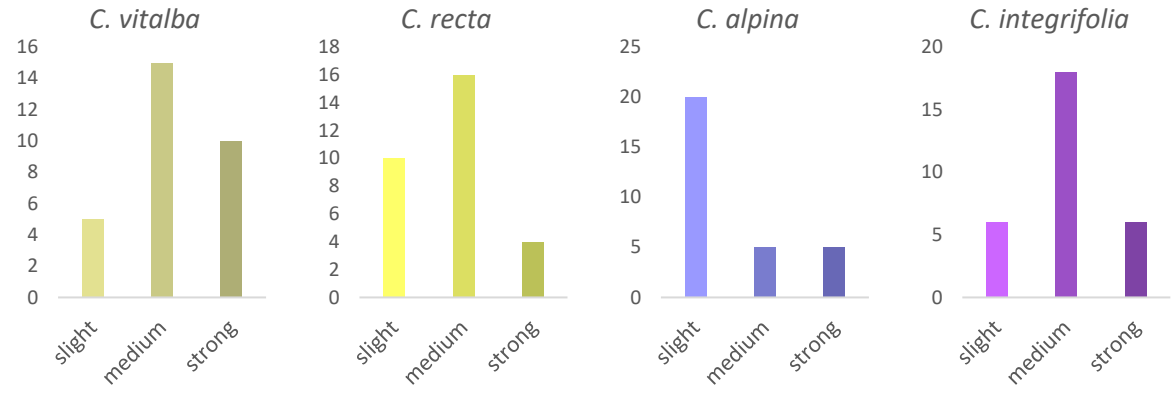


Fig. 9: Strength of floral scent in different *Clematis* species was directly smelled by nose and categorized as slight, medium or strong. *n*=30 for each species

Flowers of *C. vitalba* with cream white perianth and four (rarely five) sepals had a sepal length (values are means ± standard deviation) of 8.42 ± 1.97 mm, calyx opening of 11.84 ± 3.24 mm and calyx diameter of 16.66 ± 4.28 mm. The entire androecium had a length of 8.84 ± 1.46 mm and the gynoecium of 7.89 ± 1.14 mm, the total number of stamens (opened and closed combined) was 52.68 ± 10.0 and number of pistils was 21.53 ± 3.52 (Tab. 3). In seven out of 30 flowers, nectar was detected. Nectar standing crop was approximately 0.1µl per flower. *C. recta* is similar to *C. vitalba* in overall floral appearance, with cream white perianth and four (rarely five) sepals. The length of sepals was (M ± SD) 9.37 ± 1.84 mm with a perianth opening of 13.70 ± 2.73 mm and a calyx diameter of 19.84 ± 4.40 mm. The entire androecium with approximately 6.55 ± 1.67 mm long, the gynoecium 5.46 ± 1.15 mm. The flowers had a total number of 22.77 ± 6.90 stamens and 6.67 ± 1.84 pistils (Tab. 3). It had no nectar production in the observed flowers. The flowers of *C. alpina* with violet to blue perianth have four sepals with a length of (M ± SD) 37.0 ± 6.48 mm, calyx opening 7.24 ± 3.43 mm and calyx

diameter of 32.27 ± 13.66 mm *C. alpina* is the only out of the four Austrian *Clematis* species which had staminodes covering the fertile parts of the flower (Fig. 10). These infertile staminodes are wider and larger than the fertile stamens and can be described as spathulate staminodes (Li et al., 2022). The length of the infertile androecium was 15.44 ± 1.96 mm, fertile androecium had a length of 12.88 ± 1.67 mm and gynoecium was 9.89 ± 1.80 mm long. The number of infertile staminodes was 4.87 ± 1.80, the number of fertile stamens (total) was 43.63 ± 6.44 and number of pistils was 41.03 ± 14.81 (Tab. 3). Nectar was found in 13 out of 30 flowers. 0.1 - 2.4 µl (0.75 ± 0.78) were documented and measured sugar concentration in 9 flowers was 25.11 ± 9.35 brix. *C. integrifolia* with its four violet to purple sepals had substantially larger flowers, with a sepal length of (M ± SD) 21.29 ± 5.48 mm, perianth opening of 24.35 ± 7.02 mm and perianth diameter of 33.07 ± 9.34 mm. The androecium had a length of 12.84 ± 1.41 mm and the gynoecium of 11.30 ± 1.69 mm. The number of stamens (total) was 54.3 ± 9.53 and the number of pistils 47.04 ± 12.01 (Tab. 2). Nectar was found in 12 of 30 flowers. 0.1 - 1.2 µl (0.36 ± 0.36) could be extracted and in two flowers, it was possible to measure the sugar concentration, which was 45 brix in each case.

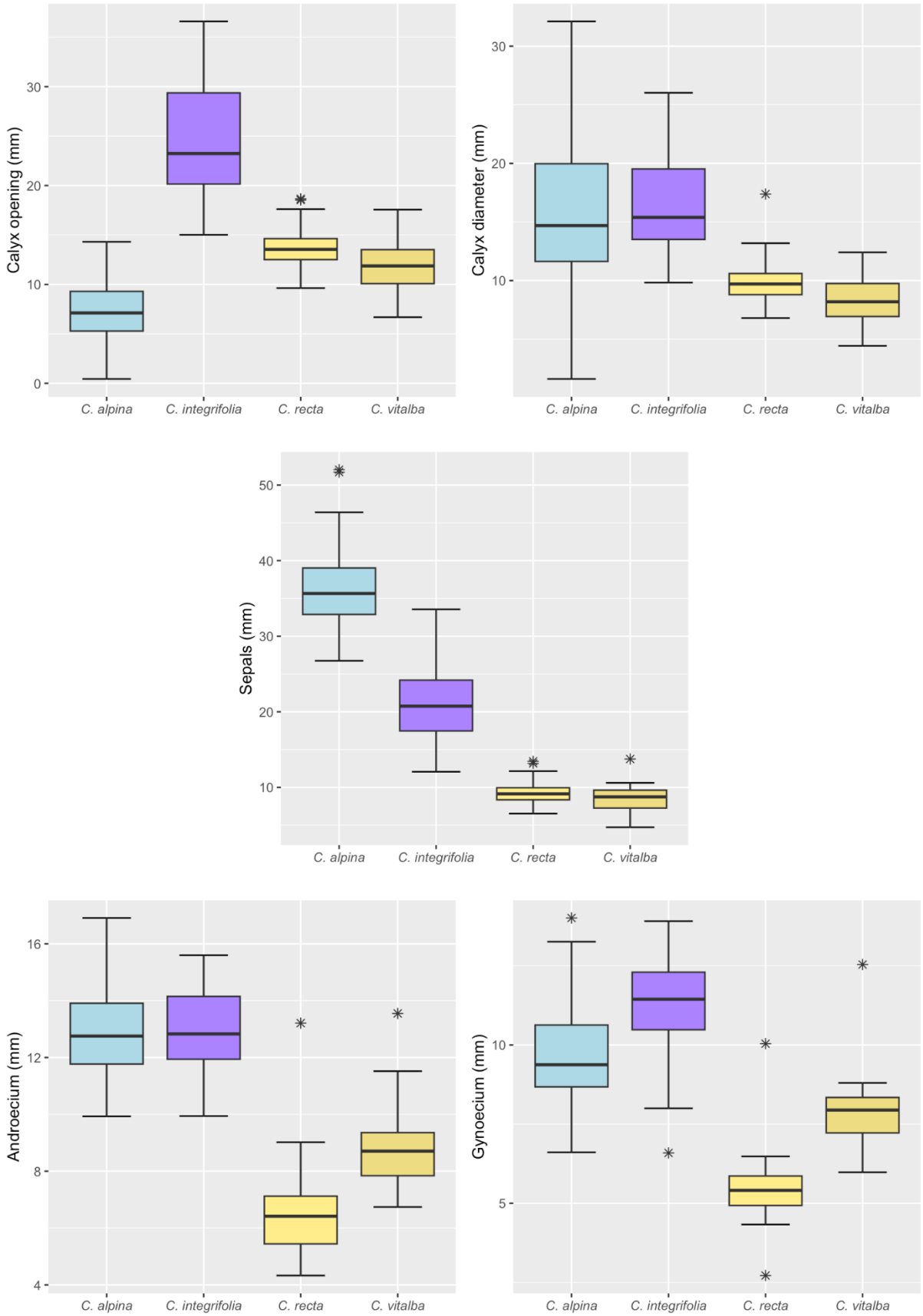


Fig. 10: Comparison of the size measurements made of the calyx (calyx opening and diameter and sepal length) and reproductive organs (androecium and gynoecium length) of *C. vitalba*, *C. recta*, *C. alpina* and *C. integrifolia* (measured in mm, values are means)

Tab. 2: Floral traits of the four *Clematis* species. Values (measured in mm) are means (± SD)

Floral traits	***C. vitalba***	***C. recta***	***C. alpina***	***C. integrifolia***
Opening of the anthers	From outer to inner	From outer to inner	From outer to inner	From outer to inner
Nectar production	✓	not found in field	✓	✓
Floral odor	✓	✓	✓	✓
Floral color	Cream white	Cream white	Blue/violet	Violet/purple
Sepal size (length)	8.42 ± 1.97	9.37 ± 1.84	37.0 ± 6.48	21.29 ± 5.48
Calyx (opening)	11.84 ± 3.24	13.70 ± 2.73	7.24 ± 3.43	24.35 ± 7.02
Calyx (diameter)	16.66 ± 4.28	19.84 ± 4.40	32.27 ± 13.66	33.07 ± 9.34
Androecium2 (length)	-	-	15.44 ± 1.96	-
Androecium (length)	8.84 ± 1.46	6.55 ± 1.67	12.88 ± 1.67	12.84 ± 1.41
Gynoecium (length)	7.89 ± 1.14	5.46 ± 1.15	9.89 ± 1.80	11.3 ± 1.69
No. spath. staminoides	-	-	4.87 ± 1.80	-
No. stamens	52.68 ± 10.0	27.77 ± 6.90	43.63 ± 6.44	54.3 ± 9.53
No. pistils	21.53 ± 3.52	6.67 ± 1.84	41.03 ± 14.81	47.04 ± 12.01

Statistical Analyses

The non-metric multidimensional scaling (NMDS) showed differences in the recorded floral traits with a stress level of 0.12 after 20 runs (k = 2) (Fig. 8). PERMANOVA showed that there is a significant difference between the four *Clematis* species *(F* = 136.52*, R2* = 0.78*, p* = 0.001*).* Post-hoc tests showed the greatest overlap of flower characteristics in *C. vitalba* and *C. recta* and *C. alpina* was the most distinct from all the other species, while *C. integrifolia* was intermediate between the other species (Tab.4). Although *C. vitalba* and *C. recta* overlapped in NMDS space, statistical analyses revealed that there is a significant difference in the morphology of the species. (Fig. 11, Tab. 3).

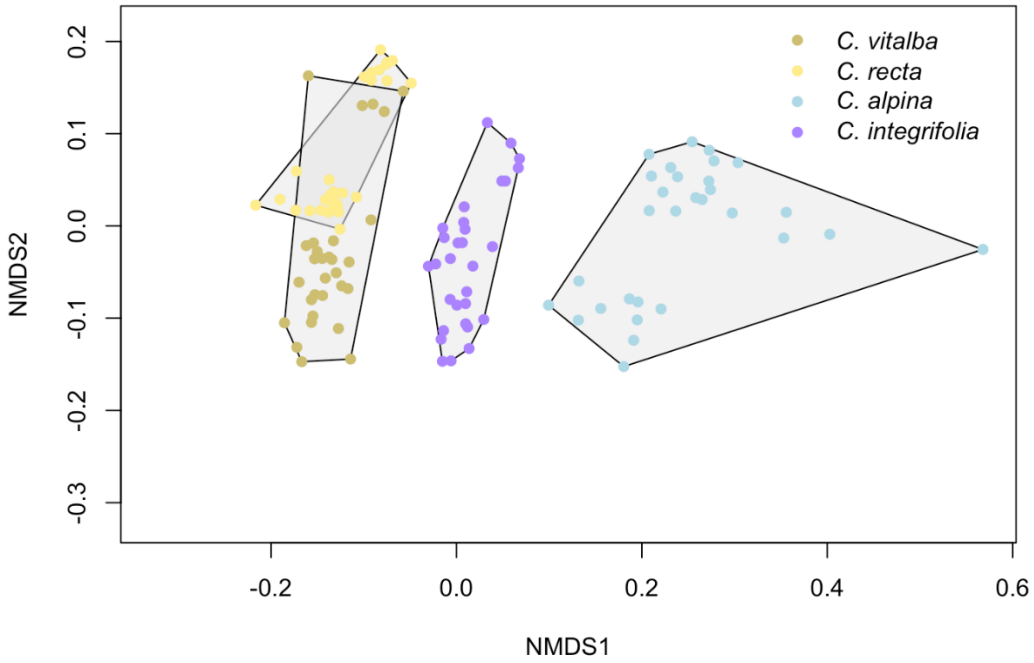


Fig. 11: Non-metric multidimensional scaling (NMDS) of floral traits (floral color, odor, sepal length, calyx opening and diameter, androecium and gynoecium length, total number of stamen and pistils) of *C. vitalba*, *C. recta*, *C. alpina* and *C. integrifolia*

Tab. 3: Pairwise comparison of differences in floral traits of the four *Clematis* species.

	F. Model	*R2*	*p. value (adjusted)*
C. vitalba vs. *C. recta*	49.02	0.46	0.006
C. vitalba vs. *C. alpina*	160.6	0.73	0.006
C. vitalba vs. *C. integrifolia*	119.93	0.67	0.006
C. recta vs. C. *alpina*	248.18	0.81	0.006
C. recta vs. *C. integrifolia*	179.74	0.76	0.006
C. alpina vs. *C. integrifolia*	59.1	0.50	0.006

Further, non-metric multidimensional scaling (NMDS) also showed a difference in floral traits of *C. vitalba* between observation sites, despite substantial overlap in the center of NMDS space (Fig. 12). The PERMOVA found a significant difference between the floral traits of *C. vitalba* in the different locations (F = 2.62, $R2$ = 0.16, p = 0.029) and the post-hoc test showed that there is a significant difference between individuals in Bärenschützklamm and Schloßhof/Marchegg (F = 4.19, $R2$ = 0.19, p = 0.03), but no significant difference between individuals in Bärenschützklamm and Gumpoldskirchen (F = 2.45, $R2$ = 0.12, p = 0.21) and individuals in Gumpoldskirchen and Schloßhof/Marchegg (F = 1.39, $R2$ = 0.07, p = 0.74) (Fig. 12). Direct comparison of the floral traits of *C. vitalba* at the different locations reveals only slight deviations in the mean values; only the number of counted stamens differs somewhat

more between *C. vitalba* in the Bärenschützklamm (61.1 ± 5.7) and Schloßhof (44.6 ± 10) (Fig. 13).

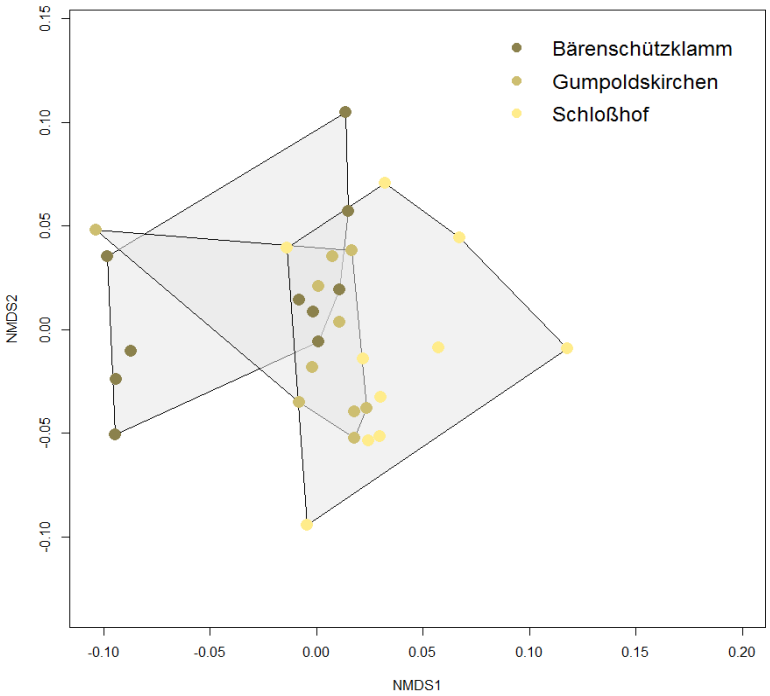


Fig. 12: NMDS of floral traits of *C. vitalba* in the different study locations (Bärenschützklamm, Gumpoldskirchen and Schloßhof/Marchegg)

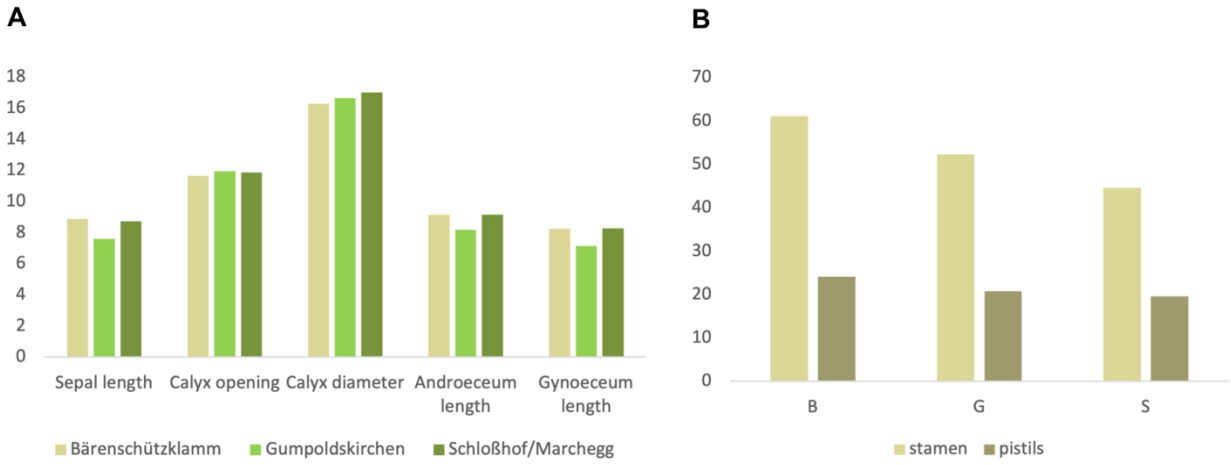


Fig. 13: Comparison of floral characteristics of *C. vitalba* flowers at the different locations Bärenschützklamm (B), Gumpoldskirchen (G) and Schloßhof (S). **A** shows the sepal length, calyx opening and diameter, length of the androecium and gynoecium (measured in mm, values are means) and **B** compares the number of counted stamens and pistils (mean) per flower at the different locations

Scanning electron microscopy

On the stigmas examined with the scanning electron microscope (SEM), pollen was found on two of the four *Clematis* species. All species had pistils with long hairs at the basal part, which became shorter towards the stigma area. On all pistils, a strip of thickened cells

can be seen, which seems to be the receptive part of the stigmas. On *C. vitalba* and *C. integrifolia,* pollen grains were found on pistils of young and of old flowers (Fig. 14 and Fig. 15). No pollen was found on *C. recta* and *C. alpina*, neither on the young nor on old stigmas examined (Fig. 16).

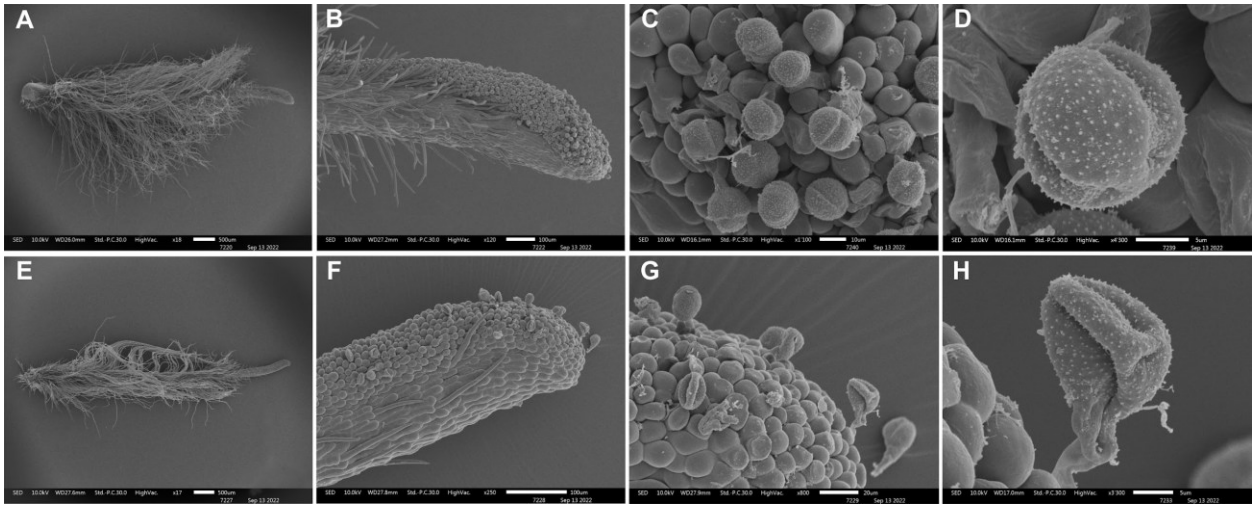


Fig. 14: SEM images of the pistils of *C. vitalba*, with stigmas of a young (**A - D**) and an old (**E - H**) flower each with pollen grains on it.

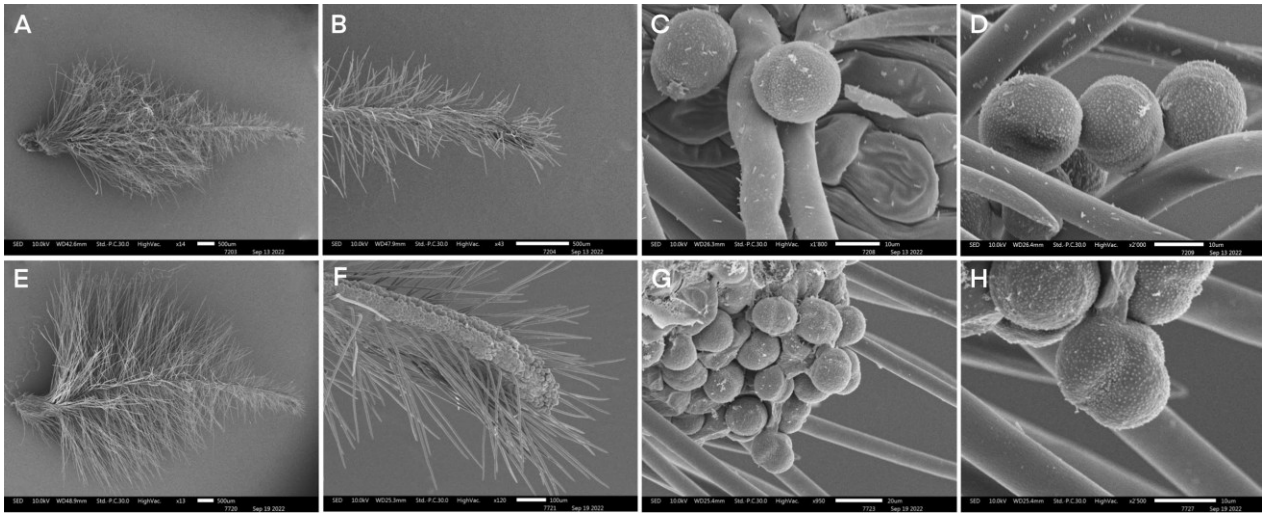
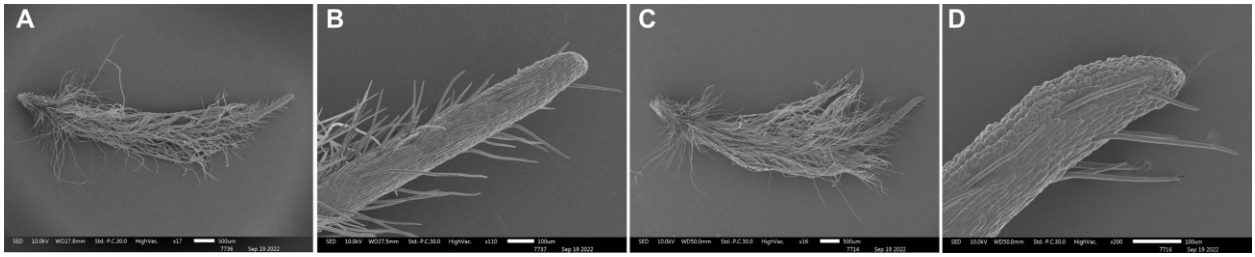


Fig. 15: SEM images of pistils of *C. integrifolia*, showing stigmas of young (**A - D**) and old (**E - H**) flowers, each containing pollen grains



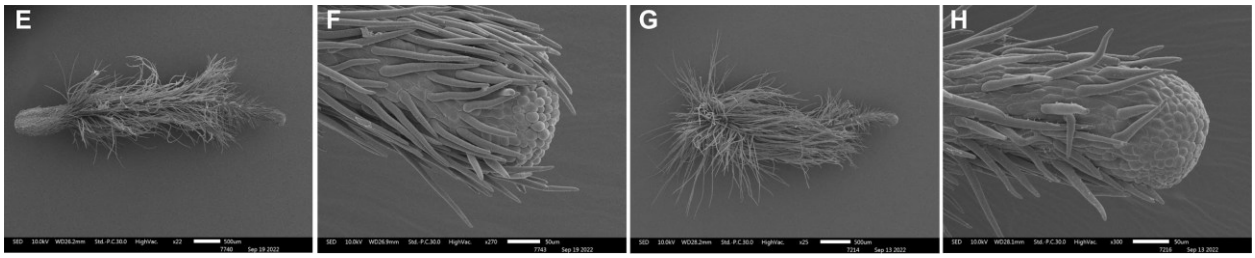


Fig. 16: On images made by SEM no pollen was found on stigmas of *C. alpina* and *C. recta.* **A, B** (*C. alpina*) and **E, F** (*C. recta*) showing stigmas from young flowers and **C, D** (*C. alpina*) and **G, H** (*C. recta*) old flowers

Pollinators

A total of 15 hours of pollinator observations were carried out for *C. vitalba*, *C. alpina and C. integrifolia* each, for *C. recta,* 17.5 observation hours were made. *C. vitalba* was equally observed for 5 hours in Bärenschützklamm, in Pfaffstätten and in Schloßhof/Marchegg. *C. recta* was observed for 11 hours in Gumpoldskirchen, 4 hours in Pfaffstätten and 2.5 additional hours in Schloßhof. 15 out of 15 observation hours on *C. alpina* were completed in Bärenschützklamm, the same applies for *C. integrifolia* in Schloßhof.

When looking at the absolute pollinator numbers, there is a strong relationship between the number of flowers observed and total abundance of pollinator individuals in each *Clematis* species. The 2625 flowers of *C. vitalba* attracted 377 pollinator individuals and reached a mean visitation rate of 0.13 pollinators per flower per hour. The 1015 flowers of *C. recta* were visited by 82 pollinators, with a mean visitation rate of 0.1 insects per flower per hour. The 142 observed flowers of *C. alpina* attracted a total of 19 pollinators with a mean visitation rate of 0.1 pollinators per flower per hour. On the 109 flowers of *C. integrifolia* 59 pollinators could be found, and the mean visitation rate was 0.45.

Regarding the insect orders which were classified as pollinators on the four *Clematis* species, on *C. vitalba,* Hymenoptera had an abundance of 78%, followed by Diptera with 17%, then Coleoptera with 3% and Lepidoptera with 2% (Fig. 17, A). The visitation rates were 59% for the Hymenoptera, 34% for Diptera, 5% Coleoptera and 2% for Lepidoptera (Fig. 18, A). *C. recta* was visited by 50% Coleoptera, 21% Hymenoptera, 18% Lepidoptera, and 11% Diptera (Fig. 16, B) and visitation rates were 55% for the Hymenoptera, 42% for Coleoptera, 2% for Lepidoptera and 1% for Diptera (Fig. 18, B). 100% of the pollinators on *C. alpina* were Hymenoptera (Fig. 17/18, C). On *C. integrifolia,* Hymenoptera were also dominant with an abundance of 91%, Diptera were present with 5%, Coleoptera and Lepidoptera with 2% (Fig. 17, D). Looking at the visitation rates (visits per flower per hour), 60% of the pollinators were Hymenoptera, 33% Diptera, 4% Coleoptera and 3% Lepidoptera (Fig. 18, D).

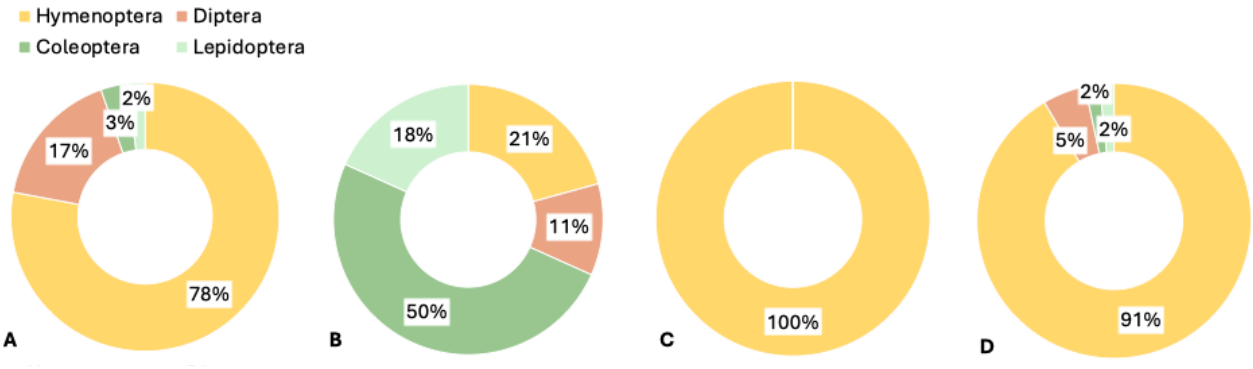


Fig. 17: Abundances (in percentages) of different insect orders found as pollinators on Austrian *Clematis* species, **A)** *C. vitalba,* **B)** *C. recta*, **C)** *C. alpina* and **D)** *C. integrifolia*

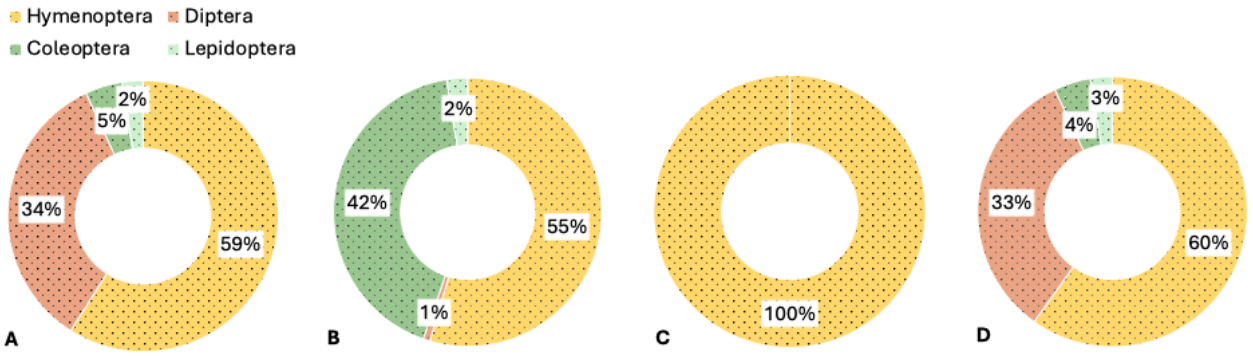


Fig. 18: Visitation rates (pollinators per flower per hour in percentages) of different insect orders on the four *Clematis* species, **A)** *C. vitalba,* **B)** *C. recta*, **C)** *C. alpina* and **D)** *C. integrifolia*

Statistical analyses

Significant differences in pollinator composition were revealed among *Clematis* species through PERMANOVA ($R2$ = 0.25, F = 4.78, p = 0.001). *C. integrifolia* and *C. vitalba* overlapped in their pollinator composition. Apart from these two species, all other species showed significantly different pollinator compositions (Tab. 5).

Tab. 5: Pairwise comparison of the four *Clematis* species using adonis2() from package 'vegan'

	F. model	*R2*	*p. value (adjusted)*
C. alpina vs. *C. recta*	3.49	0.15	0.006
C. alpina vs. *C. integrifolia*	5.39	0.22	0.018
C. alpina vs. *C. vitalba*	8.32	0.28	0.006
C. recta vs. C. *integrifolia*	5.00	0.19	0.018
C. recta vs. *C. vitalba*	1.68	0.07	0.036
C. integrifolia vs. *C. vitalba*	4.66	0.17	0.096

The comparison of the overall visitation rates between the four *Clematis* species showed that *C. integrifolia* had the highest visitation rate per flower per hour among all species (Fig. 19). According to the Kruskal-Wallis test, there was no significant difference ($X^2 = 4.054$, $p = 0.2557$) in visitation rates between *Clematis* species.

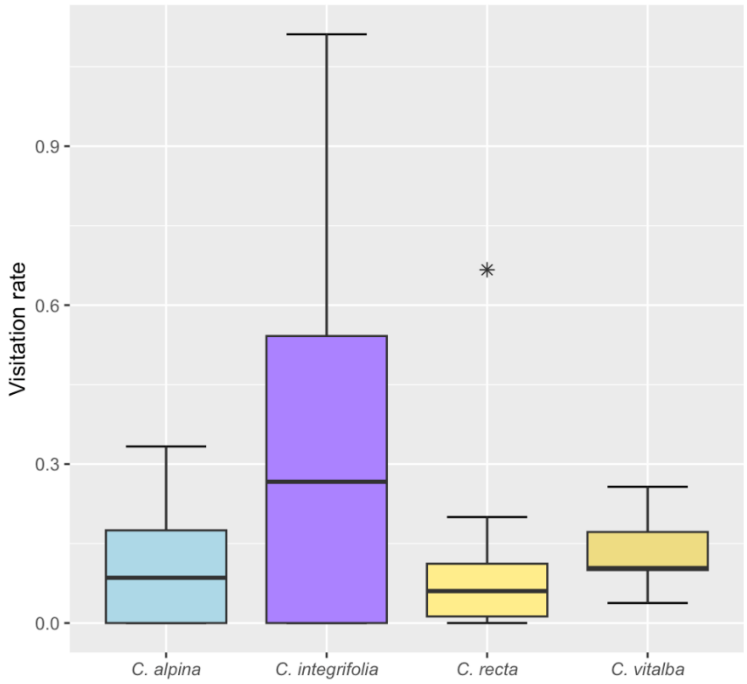


Fig. 19: Box plot comparing the differences in visitation rates among *Clematis* species, with *C. integrifolia* showing the highest visitation rates among all species. Outlier data point (asterisk) represents a patch with high visitation rate on *C. recta*

Pollinators in detail

A detailed table with abundance and visitation rate of all observed pollinators on each *Clematis* species can be found in the appendix (App. 1, 2, 3 and 4), which also contains pie charts with frequency and visit frequency to illustrate the differences in pollinator diversity between the *Clematis* species (App. 5, 6, 7 and 8).

Exploring pollinator abundances beyond the order level, on *C. vitalba,* across all observation sites combined, 64.2% of pollinators were *Apis mellifera*, 16.7% Diptera, including mainly different species of hoverflies (among others *Episyrphus balteatus*, *Sphaerophoria scripta*, *Volucella pelluscens*), genus *Pollenia* (Polleniidae), family Calliophoridae (e.g. *Lucilia sericata*), family Bombylidae (e.g. *Systeochus ctenopterus*) and others. 9.5% of pollinators came from the bee genus *Lasioglossum/Halictus* (Hymenoptera), 4.2% were other Hymenoptera including *Polistes dominula* (Vespidae), genus *Heriades* and *Megachile* (Megachilidae), *Hylaeus* (Colletidae), *Bombus pratorum* and *B. pascuorum* (Apidae), 3.2% Coleoptera, including families Cerambycidae (*Judolia ericata, Plagionotus floralis,*

Stictoleptura rubra), Burprestidae (*Anthaxia*) and some others (App. 4). 2.1% were Lepidoptera, with members of the Pieridae, Noctuidae (*Emmilia trabealis*), Nymphalidae (*Argynnis paphia*) and Crambidae (*Pyrausta falcatalis*) among others (Fig. 20, Fig. 22, a table of all pollinators can be found in App. 1).

A separate analysis on the differences in pollinator composition across the three observation sites of *C. vitalba* showed that pollinator compositions differed within the species depending on the site. In Bärenschützklamm pollinators were 78.7% *Apis mellifera*, 9.2% genus *Lasioglossum/Halictus* (Hymenoptera), 8.0% Diptera (Syrphidae), 2.0% Coleoptera (*Stictoleptura rubra*, *Pachytodes cerambyciformis*), 1.2% other Hymenoptera (*Bombus*) and 0.8% Lepidoptera (*Pyrausta falcatalis*). In Gumpoldskirchen/Pfaffstätten, there were 47.1% *Apis mellifera*, 17.6% Diptera (different Syrphid species, genus Lucilia, family Bombyliidae and Sacrophagidae), 14.7% genus *Lasioglossum/Halictus* (Hymenoptera), 8.8% other Hymenoptera (family Megachilidae and Vespidae), 7.4% Coleoptera (members of Burprestidae, Cerambycidae, Chrysomelidae, Oedemeridae and Scarabeidae) and 4.4% Lepidoptera (family Pieridae and Noctuidae). The pollinator composition in Schloßhof was 52.5% Diptera, including diverse families (e.g. Bombylidae, Calliphoridae, Muscidae, Polleniidae, Rhiniidae, Syrphidae, Trachinidae), 23.7% *Apis mellifera*, 11.9% other Hymenoptera (*Polistes dominula* and genus *Hylaeus*), 5.1% Lepidoptera, including family Pieridae and *Argynnis paphia* (Nymphalidae) and as well as the genus *Lasioglossum/Halictus* (Hymenoptera) and 1.7% Coleoptera (Fig. 21).

The pollinators observed on *C. recta* were 41.5% different Coleoptera, including the families Cerambycidae (*Judolia ericata* and *Pseudovadonia livida*), Scarabeidae (*Cetonia aurata* and *Oxythyrea funesta*), Melyridae (*Dasytes*), Tenebrionidae (*Podonta*), Burprestidae (*Anthaxia*) and Scraptiidae (*Anaspis*), 18.3% Lepidoptera, including *Maniola jurtina* and *Melanargia galathea* of the family Nymphalidae, *Pancalia leuwenhoekella* (Cosmopterigidae) and members of the Pieridae. There are 17.1% different Hymenoptera, 11% Diptera, including family Muscidae and Syrphidae (*Episyrphus* and *Sphaerophoria* scripta), 8.5% was genus *Oedemera* within the Coleoptera and 3.7% genus *Lasioglossum/Halictus* (Hymenoptera) (Fig. 20, Fig. 23, table of all pollinators in App. 2).

Bumblebees are the most common Hymenopteran pollinators on *C. alpina.* Seventy-three percent of the pollinators on *C. alpina* were *Bombus pascuorum*, 10.5% each *B. hortorum* and *B. pratorum*, and 5.3% *B. terrestris* s.l. (Fig. 20, Fig. 24, A-C, table of all pollinators in App. 3).

On *C. integrifoila,* 79.7% of all pollinators were *Apis mellifera*, 11.9% other Hymenoptera including *Bombus terrestris* s.l., *B. sylvarum* and *Xylocopa violacea*, 3.4% Diptera from genus *Stomorhina,* and 1.7% each other Diptera (Syrphidae), small Coleoptera

(not identified) and Lepidoptera (Noctuidae, *Emmilia trabealis*) (Fig. 20, Fig. 24, D-H, table of all pollinators App. 4).

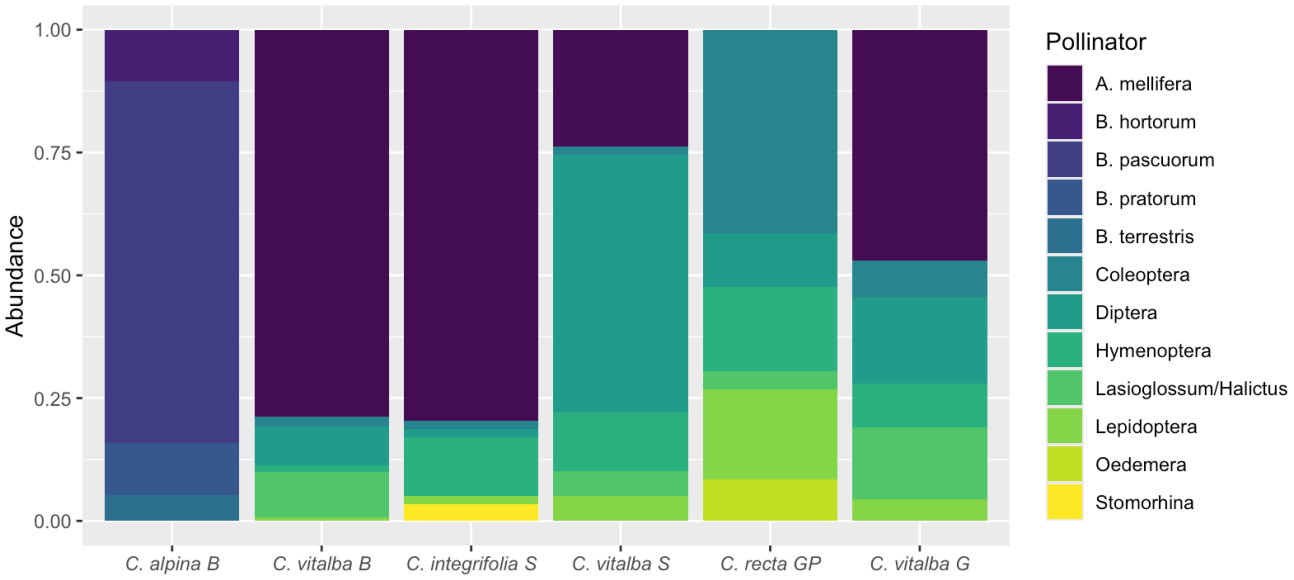


Fig. 20: Pollinator composition (main pollinators highlighted separately) of all four *Clematis* species on their observation sites and *C. vitalba* separately for all sites (Bärenschützklamm (B), Schloßhof (S), Gumpoldskirchen/Pfaffstätten (GP/G)).

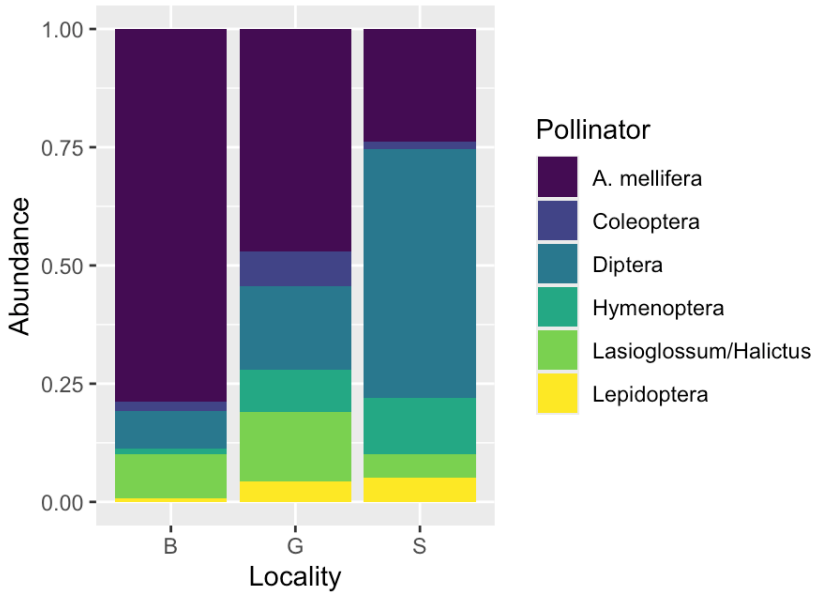


Fig. 21: Pollinator abundances (in percentages) on *C. vitalba* separated according to their different observation sites (Bärenschützklamm (B), Gumpoldskirchen (G), Schloßhof (S)).

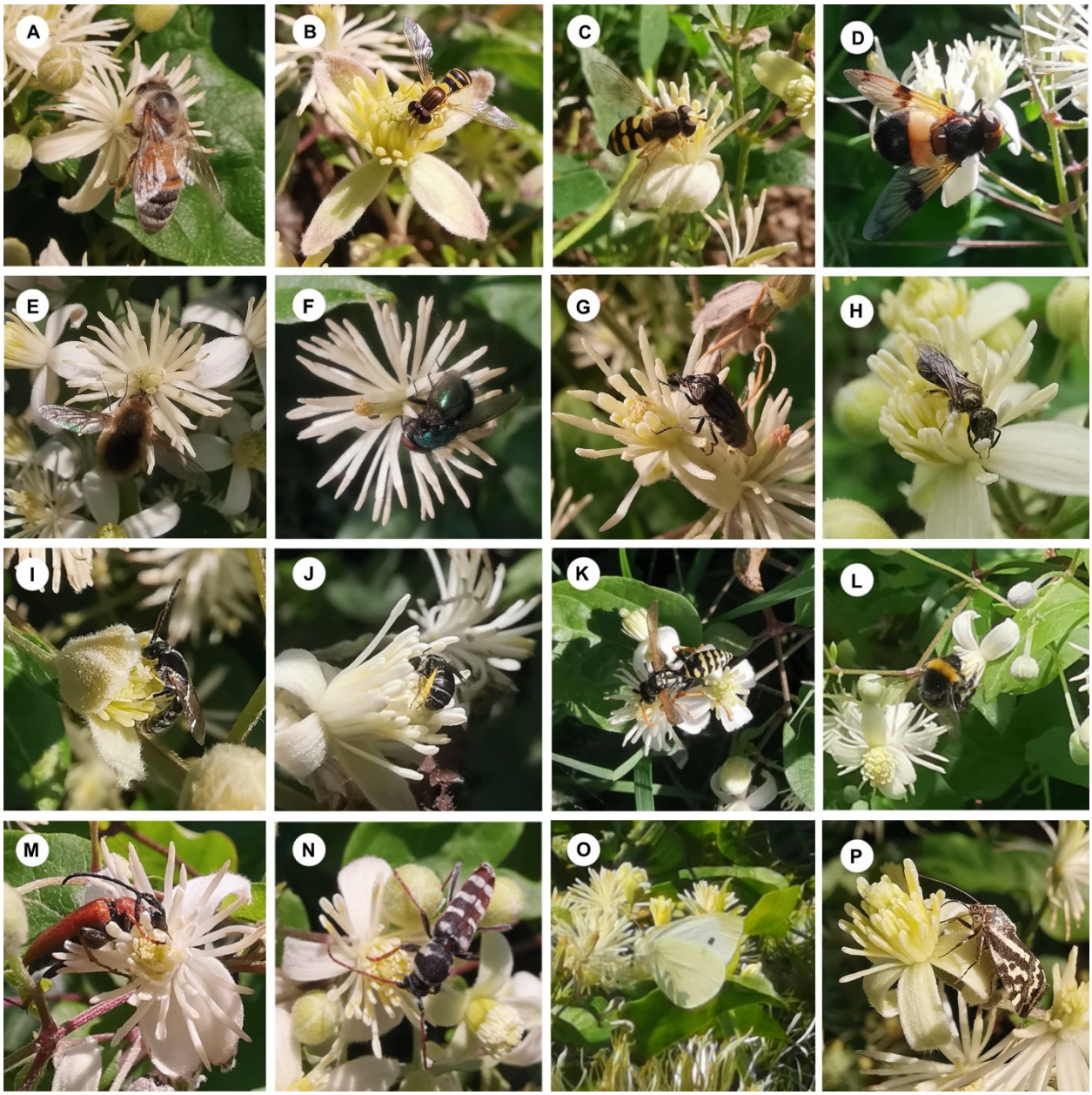


Fig. 22: A selection of pollinators on *C. vitalba*: **A**: dominating pollinator *Apis mellifera* (Hymenoptera). **B-G:** different pollinators of the order Diptera; **B:** *Sphaerophoria scripta*, **C:** genus *Eupeodes*, **D:** *Volucella pelluscens* of the family Syrphidae; **E:** *Systoechus ctenopterus* (Bombylidae); **F:** genus *Lucilia* (Calliphoridae); **G:** *Stomorhina lunata* (Rhiniidae). **H-J:** members of the order Hymenoptera; **H, I:** genus *Halictus/Lasioglossum* (Halictidae); **J:** genus *Heriades* (Megachilidae); **K:** *Polistes dominula* (Vespidae), **L:** *Bombus terrestris* s.l. (Apidae). **M, N:** Coleoptera feeding on pollen and nectar; **M:** *Stictoleptura rubra* (Cerambycidae); **N:** *Plagionotus floralis* (Cerambycidae). **O, P:** observed Lepidoptera; **O:** genus *Pieris* (Pieridae); **P:** *Emmilia trabealis* (Noctuidae)

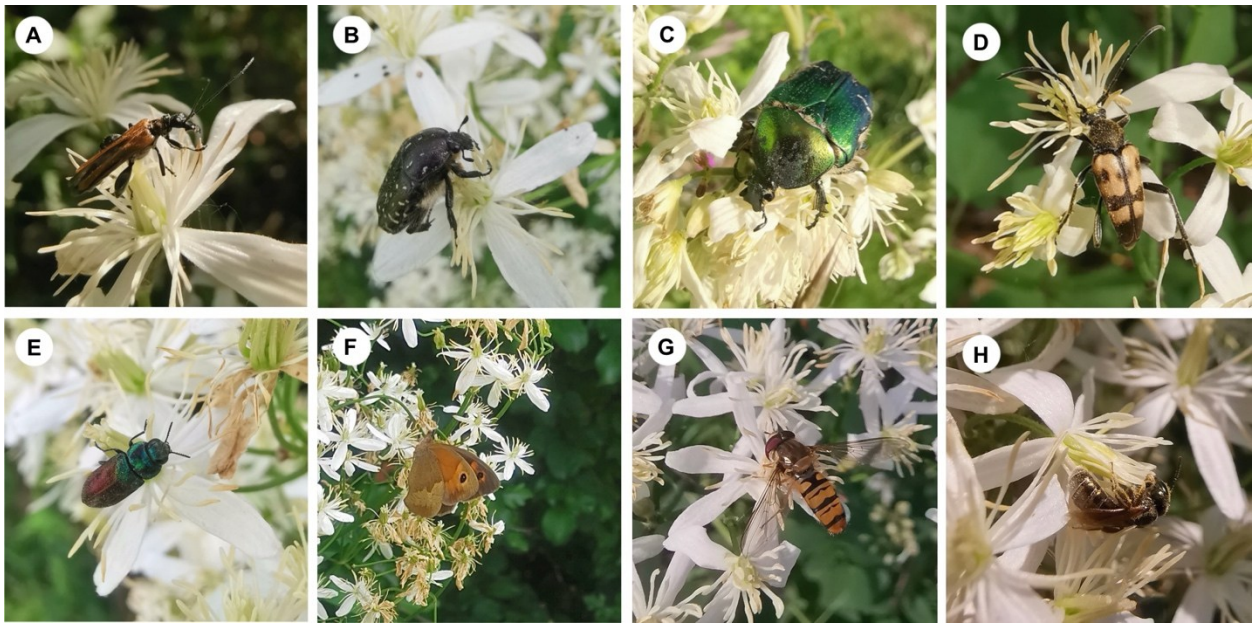


Fig. 23: Different pollinators observed on *C. recta*. **A-E:** the dominating order Coleoptera, with different representatives feeding on pollan and nectar: **A:** *Oedemera femorata* (Oedemeridae); **B:** *Oxythyrea funesta* (Scarabeidae); **C:** *Cetonia aurata* (Scarabeidae); **D:** *Judolia erratica* (Cerambycidae); **E:** genus *Anthaxia* (Burprestidae); **F:** *Manolia jurtina* (Nymphalidae, Lepidoptera); **G:** *Episyrphus balteatus* (Syrphidae, Diptera); **H:** *Halictus/Lasioglossum* (Halictidae, Hymenoptera)

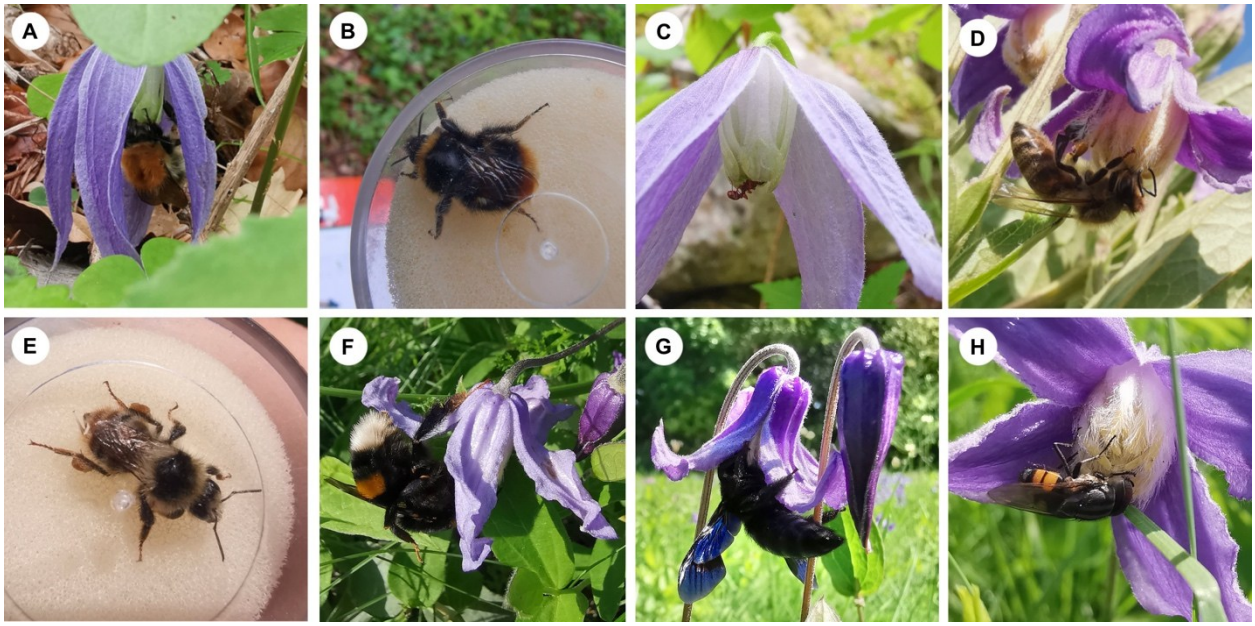


Fig. 24: A-C: Pollinators and floral visitors found on *C. alpina* of the genus *Bombus* (Apidae, Hymenopter). **A:** the most abundant pollinator *B. pascuorum*; **B:** *B. pratorum*; **C:** visitor (Formicidae) on a flower, trying to reach rewards. **D-H:** pollinators on *C. integrifolia*. Different Hymenoptera, **D:** *A. mellifera* as the dominating pollinator; **E:** *Bombus sylvarum*, **F:** *B. terrestris* s.l. and **G:** *Xylocopa violacea* (Apidae); **H:** *Stomorhina lunata* (Rhiniidae, Diptera)

Pollinators at night on *C. vitalba* and *C. recta*

During nighttime observations on June 16, 2021 in Pfaffstätten, no nocturnal pollinators were observed on *C. recta*. Only nymphs of the order Orthoptera and representatives of the order Dermoptera were found on sterile parts of the plant; these were classified as visitors, because no interaction with reproductive organs could be observed.

The nocturnal observations of *C. vitalba* on August 17, 2021 in Marchegg (close to Schloßhof) showed the presence of various nocturnal pollinators, including mostly moths, as well as a representatives of the order Neoptera. A total of 10 individuals of 7 different species were observed, with Turnip moth (*Agrotis segetum*, Noctuidae) occurring four times (Tab. 6 and Fig. 20).

Tab. 6: Nocturnal pollinators on *C. vitalba* in Marchegg (Schloßhof), including one representative of the order Dermaptera and six of the order Lepidoptera

Order	Family	Genus / species	Abundance
Dermaptera			1
Lepidoptera	Aluctidae		1
Lepidoptera	Crambidae		1
Lepidoptera	Noctuidae	*Agroits segetum*	4
Lepidoptera	Noctuidae	*Anarta trifolii*	1
Lepidoptera	Noctuidae	*Autographa gamma*	1
Lepidoptera	Noctuidae	*Mythimna albipuncta*	1

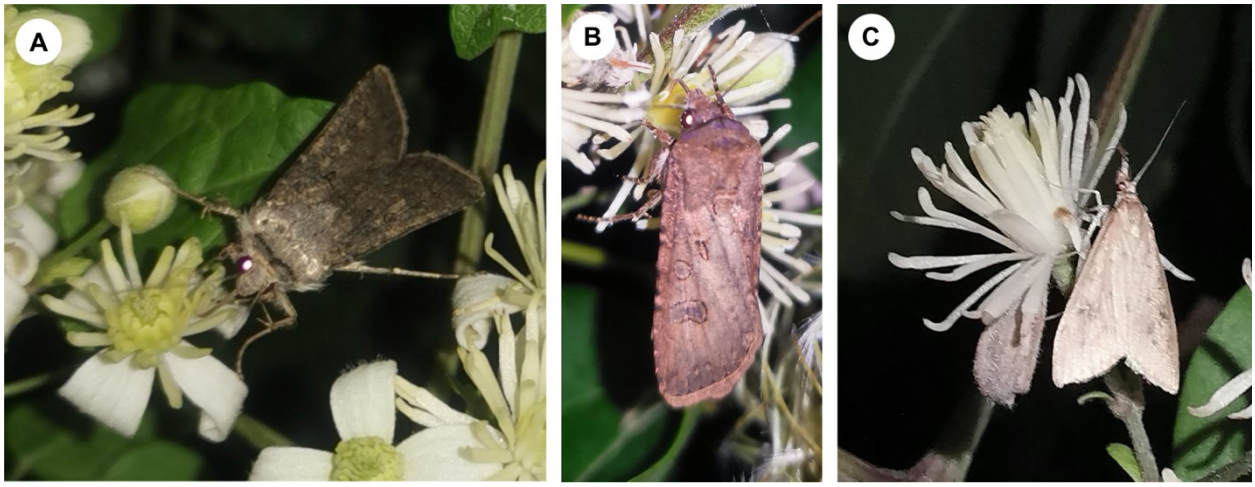


Fig. 25: Different moths drinking nectar on *C. vitalba* at night in location Schloßhof/Marchegg. **A, B:** *Agrotis segetum* (family Noctuidae) and **C:** family Crambidae

Discussion

In this study the flower morphology and pollinators of the Austrian *Clematis* species (*C. vitalba, C. recta, C. alpina* and *C. integrifolia*) were investigated, aiming to test hypotheses regarding their pollinators, associated pollination syndromes and reproductive strategies.
Pollination syndromes can be described along a continuum from generalized to specialized, rather than as discrete categories. Classical pollination syndrome theory proposes that certain floral traits – such as flower morphology, color and nectar characteristics – are shaped by adaption to particular pollinator groups (Faegri & van der Pijl, 1979; Fenster et al., 2004). Based on previous studies of *Clematis* (Jiang et al, 2010; Tomas et al, 2022; Redmond & Stout, 2018; Knuth 1898), it was hypothesized that species with dish-like flowers (*C. vitalba* and *C. recta*) would exhibit a generalist pollination syndrome, attracting a broad range of insect visitors, whereas bell-shaped and tubular flowers (*C. alpina* and *C. integrifolia*) would be more specialized toward long-tongued pollinators, particularly bumblebees. *C. vitalba* and *C. recta* attracted a wide variety of insects, particularly Diptera, Hymenoptera and Coleoptera, supporting their classification as generalist flowers. In contrast, *C. alpina* was visited exclusively by bumblebees, indicating higher degree of specialization. Observations of *C. integrifolia* also support a more specialized pollination syndrome, although a slightly greater diversity of pollinators was recorded. Nevertheless, the flowers were visited predominantly by larger, long-tongued Hymenoptera, with *Apis mellifera* being the most frequent visitor, while Diptera, Coleoptera and Lepidoptera were observed only occasionally. The following section discusses the observations made in the four *Clematis* species, starting with the floral traits and continuing with the floral visitors and pollinators observed on the plants, in order to subsequently combine and classify the findings of the study into an overall picture.

Floral traits

The measurements and analysis of floral traits confirmed the apparent phenotypic differences among the four *Clematis* species, with *C. vitalba* and *C. recta* differing notably from *C. alpina* and *C. integrifolia*. *C. vitalba* and *C. recta* have cream white and significantly smaller, spreading, dish-like flowers, *C. alpina* have bluish sepals with a bell-like shape and the violet/bluish flowers of *C. integrifolia* were tubular, both latter species with a nodding posture of the flowers.

Floral morphology

Statistical analyses revealed that the four species differ significantly from each other, which is obvious when comparing the two dish-shaped flowers to the two bell-/tubular-shaped flowers. This is also confirmed by the high *F* values (>160), which are lower when comparing more similar species (*C. vitalba* vs. *C. recta* and *C. alpina* vs. *C. integrifolia* (*F* = <60)). These

differences between the more similar species could be explained by the fact that the sepals curl up noticeable from the tips during anthesis in *C. vitalba* and *C. integrifolia* and thus appear shorter in measurements. A clear difference between *C. vitalba* and *C. recta*, which is not obvious at first sight, is the lower number of stamens (about half as many) and pistils (only a third as many) in *C. recta* (see Tab. 2).

In *C. integrifolia*, sepals form a tube in early flowering stages that opens during anthesis, potentially changing pollinator accessibility. Studies on *C. stans* in China showed that temporal changes in calyx tube length led to shifts in pollinators, related to proboscis length (Dohzono & Suzuki, 2002; Dohzono et al., 2004). However, recent work suggest that these patterns may not solely reflect morphological matching but could also result from pollinator competition and resource partitioning (Temeles & Dalsgaard, 2016). The present study did not distinguish between floral stages in pollinator observations, which prevents conclusions about stage-specific visitation. Even if unintentionally, observation focused mainly on fully opened flowers, and it seemed that, at least the dominant pollinator, *Apis mellifera*, preferred open flowers. Individuals collected pollen either from the tips of the androecium or by positioning themselves laterally and inserting their proboscis between the stamens to access nectar at their base, which would not be possible in flowers with long tubes. However, visits to young flowers cannot be excluded. The observed changes in floral morphology therefore suggest calyx-length-dependent pollinator assemblages and could be addressed in future studies of *C. integrifolia*.

In *C. alpina*, it was found that sterile spathulate staminodes additionally enclose the fertile stamens and gynoecium. In the sect. *Atraegene* L. – the section *C. alpina* belongs to (Yang et al., 2009) – *Clematis* exhibits differently shaped staminodes, which can have various functions. These include attracting pollinators through coloration similar to sepals, nectar production, protecting the carpels, or having no specific function (Li et al., 2021). Li et al. (2021) examined the different stamens in *Clematis macropetala* L. and suggested that the fertile staminodes serve a visual attraction for insects and demonstrated nectar secretion on their spatulate staminodes. These spathulate staminodes are also found in *C. alpina*, but no nectar production was observed on them in the flowers studied in the field. However, they enclose the reproductive parts of the flower in such a way that they at least serve protection and additionally limit access to the flower, thus contributing to a specialized syndrome that primarily allows long-tongued insects to reach the rewards in the center of the flower.

Reproductive traits

In all four species, anther dehiscence occurs from the outside of the androecium to the floral center, which is consistent with the descriptions of Knuth (1898). Receptivity of stigmas could be documented in both freshly opened (no/few anthers dehisced) and old flowers

(most/all anthers dehisced). These observations suggest the possibility of cross-pollination from the beginning of anthesis and allow for self-pollination at the end of the flowering period. Knuth (1898) described *C. vitalba* as a slightly protogynous flower and *C. recta* as a flower showing slight protandry. This was confirmed for *C. vitalba*, as in freshly opened flowers, the stigmas protruded slightly from the androecium and receptivity tests were already positive in flowers where all anthers were still closed. In *C. recta*, on the other hand, the stamens were always slightly standing above the stigmas. Nevertheless, the stigmas were receptive in both freshly opened and older flowers, which does not support the protandry reported by Knuth. This suggests that his statement may have been based on superficial observations on flowers only. In *C. alpina* the stamens usually extend beyond the stigmas during the entire anthesis, and in *C. integrifolia*, stigmas were still hidden in the androecium at the beginning of anthesis, but in older flowers, they protrude from it, which facilitates self-pollination, as Knuth (1898) has already described. In addition, the increased accessibility of the stigma at this floral stage allows for potential pollination by other insect groups (e.g., Diptera and Coleoptera), which visit the flowers as pollen-feeding visitors (see section “Pollinators“ for further discussion).

In their study, Jiang et al. (2010) experimentally investigated the breeding systems of three *Clematis* species. They found that *C. akebioides* and *C. rhederiana*, with bell-shaped flowers and anthers dehiscing from the outside inward, exhibit a high potential for self-pollination. In contrast, *C. chrysocoma*, with dish-shaped flowers and anther dehiscence from inside outward, showed a very low potential for self-pollination, indicating a strong reliance on cross-pollination for successful reproduction. In all three species, both seed set and fruit production were reduced under self-pollination compared to natural pollination. This pattern seems to make sense in the light of generalized versus more specialized pollination syndromes: plants with higher degree of specialization are more vulnerable to pollinator limitation, and a positive relationship has been observed between specialization and the potential for self-pollination (Pérez et al., 2009). The bell-shaped and more specialized flowers, which – due to their floral morphology – rely on long-tongued pollinators, use self-pollination as a “backup” when cross-pollination fails; the generalist flower, on the other hand, does not rely on this mechanism to the same extent (Jiang et al. 2010). Since in this present study experimental analyses of the breeding system were not made, this would be an interesting addition for future research on Austrian *Clematis* species. All investigated species exhibit traits indicative of at least a potential for self-pollination, such as anther dehiscence progressing from the outside inward and stigma receptivity until the end of the flowering period. However, the extent of this potential may differ between the two generalist and the two more specialized species.

For *C. vitalba* and *C. integrifolia*, the photos taken with scanning electron microscopy (SEM) confirmed that pollen (partially germinated) was present on the stigmas of both young

and old flowers. No pollen was found on *C. recta* and *C. alpina*. The patches of these two species studied in the field were small with few flowers and located further apart, which could explain a lower number of pollinators and thus also the absence of pollen on stigmas. However, because only one young and old pistil per species was examined, no definitive conclusions can be drawn, apart from proving that, at least in *C. vitalba* and *C. integrifolia*, young stigmas do already receive pollen.

Floral rewards & scent

Nectar, particularly nectar volume and concentration are important traits associated with animal pollination and pollination syndromes (Fenster et al., 2004). Rewards in the form of pollen and/or nectar could be detected in all species, with the exception of *C. recta* where no nectar was found. In all other species, nectar secretion was found on the inner, basal part of the stamens. No bagging treatments were made, which means the nectar volume only represents the nectar standing crop, but not the actual nectar production rate of the plants. It should be added that on the days when *C. recta* was examined, high temperatures in combination with no/little cloud cover may have caused small amounts of nectar to evaporate. In the similar flower of *C. vitalba*, only a small amount (0.1µl) of nectar could be found in a few flowers (n = 7, out of 30), which may indicate that the two dish-like flowers rely more on pollen as a reward for pollinators, or small pollinators that require lower amounts of nectar. Furthermore, it would fit the picture of generalist flowers, which usually attract smaller pollinators with a lower need for nectar or pollinators in search of pollen (e.g. pollen-eating beetles and flies) (Willmer, 2011). The findings in this study also match the observatons Jiang et al. (2010) made for the dish-shaped *C. chrysocoma*, were no or only very small amounts of nectar could be found.

In *C. alpina,* the greatest amounts of nectar could be detected among the observed species, with 0.75µl (mean) per flower (n = 25, out of 30). Nectar was also found in some flowers of *C. integrifolia* (n = 12, out of 30), although the amount was slightly less than in *C. alpina* (0.36µl mean). For both species, measuring sugar concentration was possible in only a few samples due to the small amounts of nectar. Nectar of *C. alpina* had a concentration of approximately 25% (mean out of n = 9), and *C. integrifolia* had a concentration of 45% (mean out of n = 2). An explanation for the higher nectar volume could be that visitation rates in *C. alpina* were significantly lower than in *C. integrifolia*, thereby influencing the nectar standing crop.

The amount of nectar present in the bell- and tubular-shaped flowers of the Austrian *Clematis* species is consistent with the observations of Jiang et al. (2010), who found nectar volumes ranging from 0.6 to 3.0µl in *C. akebioides* and *C. rhederiana*. They provide no information regarding nectar concentration in their studies. In general, bee-pollinated plants

are often characterized by a relatively low nectar volume and a high sugar concentration (Parachnowitsch et al., 2019; Vanderlook et al., 2019). In their study, Vanderlook et al. (2019) examined various Balsaminaceae and showed that various nectar traits – including nectar volume and sugar concentration – are associated with respective pollination syndromes. Bee-pollinated flowers exhibit low nectar volumes and high sugar concentrations (compared to bird-pollinated species), whereas fly-pollinated species were found to have extremely low nectar volumes with very low concentrations. Based on the observations made in this study, it can be assumed that the open, more generalized flowers of *C. vitalba* and *C. recta* are likely less dependent on a continuous nectar supply, with pollen also representing an important floral reward. In contrast, nectar appears to play a more central role in the more specialized species *C. alpina* and *C. integrifolia*, where it likely contributes to pollinator attraction and thus reproductive success. Further studies should apply bagging treatments to flowers in order to exclude pollinators and obtain more accurate data on nectar traits, like volume and sugar concentration, across the different species.

The disc-shaped flowers of *C. vitalba* and *C. recta* exhibit odor of medium strength, and so did *C. integrifolia*. The flowers of *C. alpina* are mostly slight in odor. Since scents were only directly smelled by nose, more detailed, quantitative scent data are needed for more precise analyses of floral scents in pollination syndromes and as attractory cues in *Clematis*. There is already raw data collected by Florian Etl (Department of Structural and Functional Botany, University of Vienna) which could be incorporated in the future to supplement this work. In their study of two *Clematis* species (bell-like and dish-like), Tomas et al. (2022) investigated the volatile components and found that monoterpenes were the predominant and most important components in both species, although their compositions differed. Similarly, for Austrian *Clematis* species, it could be assumed that *C. vitalba* and *C. recta* in particular exhibit a diverse scent profile to attract various pollinators, while *C. alpina* and *C. integrifolia* may contain compounds that are known to attract bees, such as linalool or beta-ocimene (Tomas et al., 2022; Cordeiro & Dötterl, 2023).

Spatial variation in floral traits

Statistical analyses showed a significant difference in floral traits of *C. vitalba* between the populations in Bärenschützklamm and Schloßhof. This could be interpreted in the context of the geographic pollinator mosaic/Grant-Stebbins model which proposes that spatial variation in pollinator assemblages can cause heterogenous selection pressures across populations (Thompson, 2005). If phenotypic differences (color or morphology) are not primarily driven by environmental factors, divergence in floral traits may be promoted by local pollinators with different morphologies or sensory systems, which could promote specification (Johnson, 2006).

Although a closer look at the data does not reveal obvious morphological differences between *C. vitalba* populations, and the relatively low *F* and R^2 values indicate that only a small proportion of the variance is explained by location, differences are nevertheless present. An obvious difference is the number of stamens that is somewhat higher in flowers of Bärenschützklamm compared to Schloßhof. At the same time, pollinator assemblages differed clearly between the study sites, especially between Bärenschützklamm and Schloßhof. While representatives of Hymenoptera, Diptera, Coleoptera and Lepidoptera visited flowers at all three sites, assemblages differed considerably between locations. Hymenoptera, particularly *Apis mellifera*, dominated Bärenschützklamm, Diptera were the predominant visitors in Schloßhof. The pollinator composition in Gumpoldskirchen was intermediate between the other locations.

A study by Gómez et al. (2009) on the generalized system of *Erysimum mediohispanicum* demonstrate that local pollinator assemblage can cause variable selection pressure on plant populations, even across relatively small geographic distances. In particular, different functional groups such as bees, flies and beetles may favor different floral traits (Fenster et al., 2004). However, in generalized systems, such selection is often heterogenous in strength and direction rather than uniformly strong (Gómez et al., 2009). To investigate whether similar pollinator-mediated selection can be found for *C. vitalba*, larger sample sizes and more detailed analyses would be required, including measurements of floral traits and fitness and information if local pollinator groups select for specific floral traits. The present data nevertheless indicate spatial variation in pollinator assemblages and together with decent morphological differentiation in floral traits this pattern is consistent with the expectation of a geographic pollinator mosaic (Thompson, 2005; Gómez et al., 2009).

Pollinators

The different floral shapes (dish-like, bell-like, tubular) of Austrian *Clematis* species suggest that they attract different types of insects for pollination. Previous studies dealing with the pollination biology of *Clematis* have shown that disc-like flowers are typically associated with generalist pollination syndromes, while bell-like or tubular flowers tend to exhibit more with specialized syndromes (Dohozono et al., 2004; Borken & Harder, 2006; Jiang et al., 2010; Tomas et al., 2022). Based on these findings and the floral traits observed in the Austrian *Clemaits* species, it was hypothesized that *C. vitalba* and *C. recta* (dish-shaped flowers) would exhibit a generalized pollination system, attracting a wide range of insect visitors, while *C. alpina* and *C. integrifolia* (bell- and tubular-shaped flowers) would show a higher degree of specialization toward long-tongued pollinators, such as bumblebees. The floral characteristics examined, together with the pollinator data collected, largely confirm this pattern, indicating

two generalist syndromes (*C. vitalba* and *C. recta*) and two more specialized syndromes (*C. alpina* and *C. integrifolia*), although the degree of specialization differs between the latter two speices.

Generalized pollination systems: *C. vitalba* & *C. recta*

Generalist syndromes are often characterized by small to medium-sized, open flowers, flat or bowl-shaped, white to cream-colored or yellowish-green with a mild to moderate odor and easily accessible rewards; nectar is often produced in relatively low volumes and can be highly concentrated (Faegri & van der Pijl, 1979). Generalization can be understood in the sense that such flowers can be visited by a wide variety of different insect groups (Ollerton et al., 2007). From the perspective of functional pollinator groups a certain degree of specialization may still be present, since such a generalized flower could favor particular groups over others; e.g. low nectar volumes may make visits less profitable for larger pollinators while still attracting smaller insects (Fenster et al., 2004). *C. vitalba* and *C. recta*, with their small, white to cream-colored flowers and easy accessible rewards, fit well within a generalized syndrome. Both species were visited by a broad spectrum of different taxa, including various species from the orders Hymenoptera, Diptera, Coleoptera and Lepidoptera. In *C. vitalba*, different Hymenoptera dominated, particularly *Apis mellifera*, followed by Diptera as well as smaller proportions of Coleoptera and Lepidoptera. Diptera were primarily represented by Syrphidae, but also a range of other families, e.g. Bombylidae, Calliphoridae, Muscidae. Diptera represent the second most important group of anthophilous insects after Hymenoptera and can play a significant role as effective pollinators (Larson et al., 2001). While Syrphidae are widely recognized as effective pollinators, non-syrphid flies, which are often overlooked, can also contribute substantially to pollination (Orford et al, 2015). Other Hymenoptera were mainly represented by small wild bees, especially from the genus Halictus/Lasioglossum.

On *C. recta* in contrast, pollinator assemblages were dominated by Coleoptera in terms of abundance, although Hymenoptera were also frequently observed, followed by less abundant Lepidoptera and Diptera. Coleoptera accounted for approximately 50% of all recorded pollinator individuals; however, visitation rates were higher for Hymenoptera. This difference can be explained by behavioral pattern, as hymenopterans typically visited multiple flowers, whereas beetles tended to stay on a single flower for longer. The presence of Lepidopera on C. recta flowers (Nymphalidae and Pieridae) suggest that nectar is likely produced, even though it was not detected in the sampled flowers. Butterflies typically visit flowers for nectar due to the morphology of their proboscis, which is adapted for liquid feeding (Willmer, 2011). Because the number of flowers of *C. recta* at the investigated sites was relatively low (except from few plants with numerous flowers), and many flowers were already

at the end of their life span, comparatively few pollinators were attracted (a correlation between the observed flowers and the number of flower visitors is evident in all species). Studies that observed other dish-shaped *Clematis* species show, that such flowers with open accessible nectar exhibit a greater diversity of pollinators, often dominated by various Diptera or Hymenoptera (Knuth, 1898; Borkent & Harder, 2006; Redmond & Stout, 2018; Tomas et al., 2022).

Specialized pollination systems: *C. alpina* & *C. integrifolia*

In contrast to the generalized species, *C. alpina* and *C. integrifolia* exhibit traits associated with more specialized pollination systems, which are characterized by a variety of traits that, through their specifications, filter a broad range of animals as pollinators and allow access to the flower and its rewards for a select group of pollinators, which pollinate these plants most efficiently (Fenster et al., 2004). Bee pollination (melittophily) is one of these syndromes and although bees are a very large and diverse group that can also differ in their behavior on flowers, it can generally be said that flowers associated with bees are often zygomorphic (though sometimes radially symmetrical) and pendant, with hidden rewards and colors ranging from bluish, violet, purple to pink, but also yellow and white (Kevan & Barker 1983; Willmer, 2011). The studied Austrian *C. alpina* and *C. integrifolia* reflect several characteristics of the above-mentioned bee specialized syndrome - and attracted mainly Hymenoptera.

C. alpina showed a high degree of specialization, as all observed pollinators belonged to the genus *Bombus*. The exclusive association with bumblebees strongly supports the hypothesis of a specialized pollination system. The temporarily low temperatures during the flowering period in May in the lower montane to alpine zone, where *C. alpina* occurs, suggest an adaptation to bumblebees, which are important pollinators in alpine environments and capable of foraging under cooler conditions (Heinrich, 1972; Bergmann et al., 1996). In contrast, other potential pollinators, such as wild bee species that prefer warmer conditions (Müller et al., 1997), are likely excluded by low temperatures. In addition, the spathulate staminodes, which are unique to *C. alpina* and enclose the reproductive parts, also limit access to the floral rewards. During fieldwork, flower visitors (Syrphidae and Formicidae) were observed being attracted by the flower, but due to the carpels being covered by staminodes, they could not reach the rewards and thus act as pollinators.

C. integrifolia was mainly visited by *Apis mellifera* and other Hymenoptera, with occasional visits by Diptera, Coleoptera und Lepidoptera. Bumblebees could therefore not be confirmed as the dominant pollinators; however, the vast majority of pollinators belonged to bees. Consequently, *C. integrifolia* appears to be primarily specialized for bee pollination, consistent with their flower characteristics, although not as strictly as seems to be the case for

C. alpina. In contrast to *C. alpina*, where pollen-bearing stamens are enclosed by sterile spathulate staminodes, the stigmas in *C. integrifolia* protrude from the androecium toward the end of anthesis. This morphological change likely facilitates access to the reproductive organs and suggest that pollination is not exclusively restricted to long-tongued insects like hymenopterans. Although the observed Diptera did not access nectar, they fed on pollen from the outer stamens and came in contact with the stigmas, potentially depositing pollen there. A similar role may also be assumed for Coleoptera species. So even though it can be assumed that bees and bumblebees might be more relevant as effective pollinators, when collecting pollen and nectar, the observations mentioned do suggest the possibility of pollination by other groups of insects, at least toward the end of anthesis. Overall, the findings for *C. alpina* and *C. integrifolia* are also consistent with other studies, where bell-shaped or tubular flowers with hidden nectar are predominantly pollinated by bees, most exclusively genus *Bombus* (Knuth, 1898; Dohzono & Suzuki 2002; Jiang et al., 2010; Tomas et al., 2022).

Statistical patterns of pollinator composition

Statistical analyses showed that the pollinator composition differed significantly for all Austrian *Clematis* species except *C. vitalba* and *C. integrifolia*. Based on obvious phenotypic differences in floral traits and previous studies about *Clematis*, it was hypothesized that *C. vitalba* (dish-shaped type) and *C. integrifolia* (tubular type) should differ in terms of their pollinators; therefore, these results are surprising. However, on the flowers of both of these species a particularly high abundance of *Apis mellifera* was observed. Honeybees were the dominant pollinators on *C. vitalba* in Bärenschützklamm, while at Schloßhof, they constituted the majority of pollinators for *C. integrifolia.*

Since the statistical similarity can most likely be explained by these high abundances of *A. mellifera*, it is worthwhile to compare the pollinator composition between *C. vitalba* and *C. integrifolia* at their shared site, Schloßhof, to find possible differences in pollinators, as proposed syndromes would suggest. While honeybees, followed by other, mainly large, long-tongued hymenopterans, are the dominant pollinator for *C. integrifolia*, Diptera clearly dominated on flowers of *C. vitalba* in Schloßhof, with *A. mellifera* being far less present, than on *C. integrifolia*. This is an important finding, as it suggests that pollinator composition is not only determined by local availability but can be explained by the concept of pollination syndromes, where flowers with different traits attract different pollinators.

Spatial variation in pollinator assemblages of *C. vitalba*

When examining the pollinators at the different locations of *C. vitalba* (Bärenschützklamm (Styria), Gumpoldskirchen and Schloßhof (Lower Austria)), clear differences become apparent, which can be attributed to the local variation in pollinator

availability and environmental conditions. Bumblebees, which can also cope with colder temperatures (Heinrich, 1972; Bergmann et al., 1996), were only found at the higher-elevation site in Bärenschützklamm. In contrast, Diptera at this site were represented exclusively by different hoverflies, which were in contrast represented by various families at the lower and warmer sites in Gumpoldskirchen and Schloßhof. Syrphidae, along Muscidae and Trachinidae, are among the flie taxa that play an important role as pollinators at higher latitudes and elevations (Kearns, 1992). In general, fly larvae often develop in moist environments (Ross, 1982), which could also explain the increased occurrence of this order at the Schloßhof site, which is located in the alluvial area of Morava River. As mentioned in the section above, at the same time, it becomes apparent that *Clematis* species with different flower types, which occur alongside *C. vitalba* at the various locations, attract different pollinators, most of which match their predicted syndromes.

For all species, a strong correlation was found between the number of flowers and the number of pollinators observed. When classifying pollinator observations in the flowers, the visitation rates (visits per flower per hour) are considered. Overall, *C. integrifolia* shows the highest visitation rates. The numerous honeybees that were dominant on its flowers, as well as bumblebees, often visited several flowers in a row, explaining high visitation rates, while having the lowest number of flowers observed, compared to the other species. It must be mentioned that in this study, all insects observed in the field that seemed to come into contact with the reproductive organs of the flowers were categorized as pollinators. The listed species should therefore be viewed with caution, as it is likely that not all insects mentioned here are actually efficient pollinators for *Clematis*. An examination of the potential pollinators for pollen grains would have exceeded the possibilities of this study, but would be useful for further research on pollination syndromes of Austrian *Clematis*.

Nocturnal pollinators

C. vitalba (Marchegg, near Schlosshof) and *C. recta* (Gumpoldskirchen) were each additionally examined for pollinators one evening after dusk. No pollinators were observed on *C. recta*, which could also be attributed to a low number of flowers and the late timing of the examinations towards the end of the flowering period. Since the study was conducted just in one night, further research would be necessary, to find possible pollinators on *C. recta*. In contrast, various moths, especially from the family Noctuidae, were observed on *C. vitalba*. The creamy/white color and the medium to strong scent of the flowers could explain the attraction of various moths on the numerous flowers of *C. vitalba* (Willmer, 2011). Further research on odors would be interesting in order to better understand the role of pollinators on clematis at night.

Conclusion

This study provides a first overview of the pollination biology of Austrian *Clematis* species. It reveals that the four species, which can be broadly divided into two groups, based on their flower characteristics (small, white and dish-shaped flowers vs. bigger, blue-violet and bell-shaped/tubular flowers), have developed two generalized and two more specialized flower types. *C. vitalba* and *C. recta*, with their open flowers, attract a diverse range of pollinators, while *C. alpina* and *C. integrifolia*, with their bell-shaped flowers, with hidden nectar, exhibit specialized pollinator patterns. The former attracts only pollinators of the genus *Bombus*, while the latter attracts a wider range of different bees (and a few other groups), which shows that pollination syndromes are not strict categories.

This study provides a basis for further research on (Austrian) *Clematis* to better understand their pollination biology. An investigation into the pollinator efficiency of the observed species would be highly beneficial to determine precisely which pollinators are actually effective as pollen vectors and therefore relevant for successful cross-pollination. A detailed analysis of the scents of the different species would also be valuable. As in the exemplary study by Jiang et al. (2010), experiments such as bagging, hand pollination, or removal-treatments on the flowers could also be carried out to investigate and understand the breeding system of the species in more detail (i.e., to assess whether self-pollination commonly occurs, given that we found stigma receptivity both in young and old flowers).

One interesting aspect that warrants further investigation is the potential shift in pollinator assemblages of *C. integrifolia* during anthesis. While changes in calyx tube length have been suggested to influence pollinator composition (Dohzono & Suzuki, 2002; Dohzono et al., 2004), the present observations indicate that the elongation of the stigmas at the end of anthesis may additionally facilitate access for other insect groups, such as Diptera and Coleoptera, potentially broadening the spectrum of effective pollinators.

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Appendix

Table of Clematis pollinators

App. 1: Abundance and visitation rate of pollinators found on *C. vitalba*

Order	Family	Genus/Species	Abundance	Visitation rate
Hymenoptera	Apidae	*Apis mellifera*	242	0,047
	Halictidae	*Lasioglossum/Halictus*	36	0,009
	Megachilidae	*Heriades*	3	0,007
	Vespidae	*Polistes dominula*	7	0,005
	Megachilidae	*Megachile*	2	0,004
	Colletidae	*Hylaeus*	1	0,0008
	Apidae	*Bombus pratorum*	1	0,0002
	Apidae	*Bombus terrestris*	1	0,0001
Diptera	Polleniidae	*Pollenia*	3	0,008
	Syrphidae	*Sphaerophoria*	8	0,007
	Bombylidae		2	0,004
	Calliphoridae	*Lucilia sericata*	6	0,004
	Rhiniidae	*Stromorhina*	5	0,004
	Calliphoridae	*Luciila*	4	0,004
	Muscidae		4	0,003
	Syrphidae		11	0,003
	Trachinidae		4	0,003
	Syrphidae	*Volucella pellucens*	4	0,001
	Bombylidae	*Systoechus ctenopterus*	1	0,0008
	Syrphidae	*Eupeodes*	1	0,0008
	Sacrophagidae		2	0,0004
	Syrphidae	*Episyrphus balteatus*	2	0,0003
	Syrphidae	*Parasyrphus*	3	0,0003
	Syrphidae	*Sphaerophoria scripta*	3	0,0003

Coleoptera	Burprestidae	*Anthaxia*	2	0,003
	Malachiidae	*Anthocomos rufus*	1	0,0006
	Cerambycidae	*Plagionotus floralis*	1	0,0005
	Oedemeridae	*Oedemera femorata*	1	0,0005
	Cerambycidae	*Stictoleptura rubra*	3	0,0005
	Cerambycidae	*Judolia erratica*	2	0,0003
	Chrysomelidae	*Bruchidius*	1	0,0002
	Scarabeidae	*Cetonia aurata*	1	0,0002
Lepidoptera	Pieridae		2	0,001
	Noctuidae	*Emmelia trabealis*	2	0,0007
	Nymphalidae	*Argynnis paphia*	1	0,0006
	Crambidae	*Pyrausta*	2	0,0002
	Erebidae	*Eilema*	1	0,0002
VR total				**0,13**

App. 2: Abundance and visitation rate of pollinators found on *C. recta*

Order		**Genus/Species**	**Abundance**	**Visitation rate**
Hymenoptera	Halictaidae	*Lasioglossum/Halictus*	3	0,049
	Apidae	*Apis mellifera*	6	0,004
	not identified		6	0,003
	Apidae	*Bombus pascuorum*	2	0,0002
Coleoptera	Oedemeridae	*Oedemera*	7	0,015
	Melyridae	*Dasytes*	3	0,012
	Scarabeidae	*Oxythyrea funesta*	7	0,007
	Cerambycidae	*Pseudovadonia livida*	8	0,004
	Scarabeidae	*Cetonia aurata*	1	0,004
	Cerambycidae	*Stictoleptura rubra*	2	0,0007
	Cerambycidae	*Judolia erratica*	4	0,0006
	Tenebrionidae	*Podonta*	5	0,0004

	Buprestidae	*Anthaxia*	3	0,0003
	Scraptiidae	*Anaspis*	1	0,0001
Lepidoptera	Pieridae		4	0,002
	Nymphalidae	*Maniola jurtina*	9	0,0008
	Cosmopterigidae	*Pancalia leuwenhoekella*	1	0,0001
	Nmphalidae	*Melanargia galathea*	1	0,00009
Diptera	Muscidae		4	0,0004
	Syrphidae		3	0,0003
	Syrphidae	*Episyrphus*	1	0,0001
	Syrphidae	*Sphaerophoria*	1	0,00009
VR total				**0,1**

App. 3: Abundance and visitation rate of pollinators found on *C. alpina*

Order	**Family**	**Genus/Species**	**Abundance**	**Visitation rate**
Hymenoptera	Apidae	*Bombus pascuorum*	14	0,073
	Apidae	*Bombus hortorum*	2	0,024
	Apidae	*Bombus pratorum*	2	0,004
	Apidae	*Bombus terrestris* s.l.	1	0,003
VR total				**0,1**

App. 4: Abundance and visitation rate of pollinators found on *C. integrifolia*

Order	**Family**	**Genus/Species**	**Abundance**	**Visitation rate**
Hymenoptera	Apidae	*Apis mellifera*	47	0,262
	not identified		3	0,036
	Apidae	*Bombus sylvarum*	2	0,054
	Apidae	*Bombus terrestris*	1	0,019
	Apidae	*Xylocopa violacea*	1	0,009
Diptera	Rhiniidae	*Stomorhina*	2	0,182

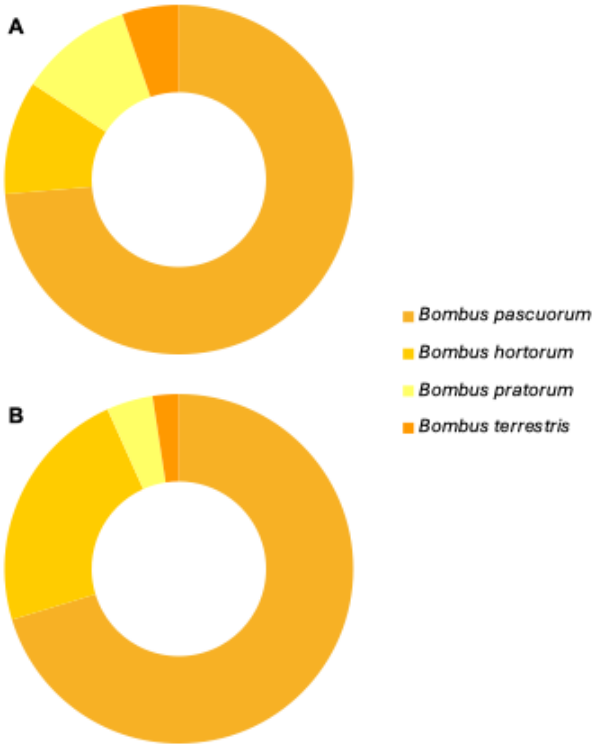
	Syrphidae		1	0,028
Coleoptera	not identified		1	0,028
Lepidoptera	Noctuidae	*Emmilia trabealis*	1	0,017
VR total				**0,45**

Pie plots of abundance and visitation rates of Clematis pollinators

App. 5: A: Pollinator diversity (abundance) and **B:** visitation rate (pollinators per flower per hour) on *C. vitalba*

App. 6: A: Pollinator diversity (abundance) and **B**: visitation rate (pollinators per flower per hour) on *C. recta*

App. 7: Pollinator diversity (abundance) and **B:** visitation rate (pollinators per flower per hour) on *C. alpina*



App. 8: A: Pollinator diversity (abundance) and **B:** visitation rate (pollinators per flower per hour) on *C. integrifolia*