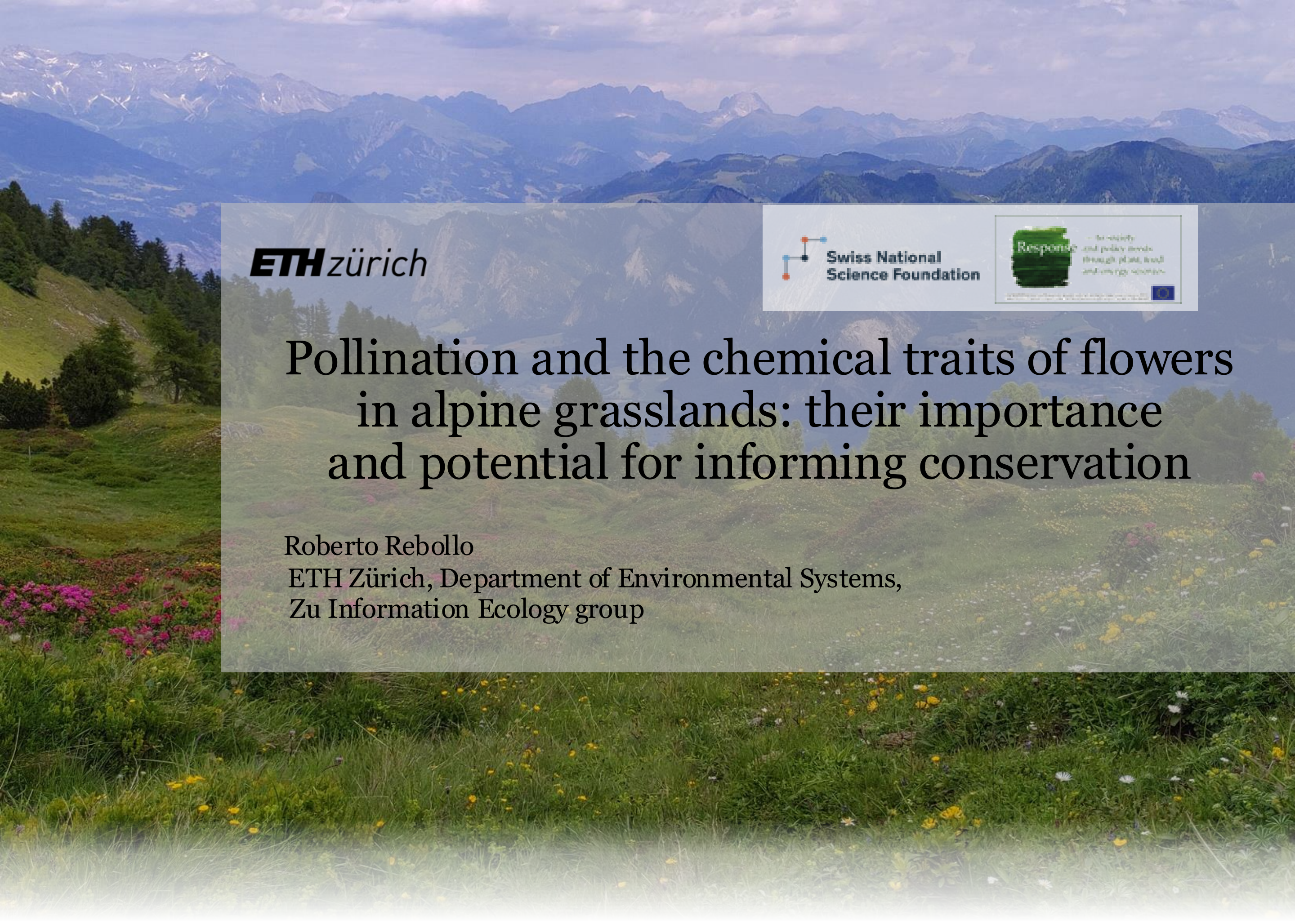

ETH zürich

Pollination and the chemical traits of flowers in alpine grasslands: their importance and potential for informing conservation

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Insect pollination is a key process in nature, which strongly contributes to biodiversity and ecosystem services. This type of pollination is strongly influenced by the chemical traits that flowers possess, with insects showing preferences to distinct flower characteristics. In the case of alpine grasslands, understanding the chemical communication can prove informative for management and conservation practices.

The role of chemical traits in mediating pollination by insects

Plant and insect interactions: the case of pollination

Flowering plants and insects are fundamental for terrestrial ecosystems. In number of species, they are two of the most diverse organism groups in the planet [1]. The evolutionary success of flowering plants and several groups of insects is attributed to the interaction with each other. Specifically, insect pollination is regarded as a key process for diversification and adaptation in both groups [2, 3, 4], leading to far-reaching consequences for living systems and societies [See **Information box 1**]. Insect pollination is strongly influenced by the chemical traits that flowers possess, such as the chemical composition of nectar and pollen, and the attraction of pollinators by displaying colors and scents.

- **Nectar**

One of the most common incentives that flowering plants offer to pollinators is nectar [5]. Nectar consists of a sugary liquid secretion and contains three main types of sugars; the monosaccharides glucose and fructose, and the disaccharide sucrose. Many insect groups have a preference for either monosaccharide-rich, or sucrose-rich nectars [6, 7]. Nectar can also contain diverse other sugars (usually in lower concentrations), amino acids, and secondary metabolites [5, 8]. These components often contribute to insect nutrition and health, and they help to modulate insect foraging behaviour [9, 10, 11].

Picture: the alpine grasslands in Calanda (Grisons) during full bloom. R. Rebollo.

Information box 1: The importance of insect pollination in alpine grasslands in the context of global change

> *"It's easy to underestimate, and impossible to exaggerate, the importance of pollinators and the pollination services they provide […] Most ecosystems of land plants, animals, fungi and microbes are ultimately reliant upon the flower-visiting activities of pollinators. They are essential both for the functioning of these ecosystems from year to year, and, in the long term, for the evolution of biological diversity."*
>
> Ollerton (2021) [62].

Pollination as a key process

Insect pollination is a key biotic interaction in land ecosystems, whose importance to ecosystems is difficult to overstate [62]. Biotic interactions, in general, are also essential components of ecosystem functioning, with most ecosystem services depending on them in some way [63]. Recognizing this critical role, pollination has been declared a strategic target for protection by the UN Conference of the Parties (COP15) [64]. Similarly, biotic interactions are a target of conservation under the Swiss Biodiversity Strategy and Action Plan [65].

Pollination importance for Biodiversity

Pollination is a critical biological process. More than 85% percent of flowering plant species are pollinated by insects [66]. Conversely, around 30% of arthropod species regularly visit flowers [67]. From the perspective of plants, pollination allows the exchange of genetic material even with distant flowers, providing with the ability to better adapt to new ecological challenges. The alpine flora is particularly vulnerable to the rapid global change [68, 69], and genetic flow between populations will be a critical factor in the survival of alpine species [70]. Concomitantly, recent decades have been marked by a quick insect decline at alarming rates [71, 72]. This change is closely related to the simultaneous change in soil use, overabundance of nitrogen compounds in soil, and climate change [73]. Additional to these threats, alpine pollinators need to cope with changes in the distribution, phenology and extinction of alpine plants [68].

Pollination importance for Ecosystem Services

The protection of interactions is far from being important only for species conservation. Pollination, when regarded as a provisioning ecosystem service, is of utmost importance, as it is strongly linked to food production [74]. Bee pollination alone is thought to directly contribute to around 30% of global crop food production [75]. Moreover, pollination supports other key ecosystem processes, indirectly enhancing other ecosystem services. Relevant for alpine grasslands, pollination supports primary productivity, nutrient cycling, pest control, and reduction of soil erosion [76, 74].

Alpine grasslands also offer spiritual and recreational ecosystem services, often generating income through tourism. Recent studies have found that open alpine grasslands attain a higher aesthetic value for the public than abandoned and reforested areas [77]. For alpine grasslands, flower color diversity and abundance are related to a higher aesthetic value [78, 79, 80]. There is a positive link between plant species diversity, amount of resources for pollinators, and flower color richness, linking several interests of conservation [81]. However, it is noted that primary productivity is negatively linked to the latter ecosystem services, suggesting that maintaining heterogeneity in management intensity is a way to maximize the benefits from diverse ecosystem services (by maintaining some patches with high productivity, while others provide a rich habitat for insects, etc.) [81].

• Pollen

In addition to nectar, pollen can also be an important nutritional reward. Pollen grains have diverse chemical components, and many insect species have developed the ability to use pollen as a valuable source of nutrients [12, 13]. For example, in the case of bees and bumblebees, pollen is as a source of essential amino acids and lipids [14] and have thus of obligate mutualists of plants. Other insects, such as flies and beetles, are also able to obtain nutrients from pollen [15].

• Color

Flower pigments are largely responsible for flower colors [16] (with only a limited variation in color being due to the microstructure of petals). Color can be important in guiding pollinators to flowering patches, and at eliciting feeding behavior at short distances [17]. Pollinators often show preferences to particular colors [18, 19], which can be innate or learned.

• Scent

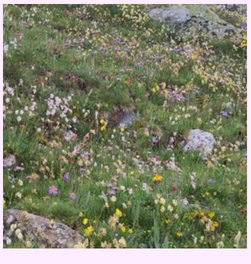
Flower scent consists of the mixture of volatile organic compounds released from flowers, often from specialised structures. Volatile organic compounds are highly diverse, resulting from multiple biosynthetic pathways, and often constrained to certain taxa [20, 21]. Insects have varying sensitivity and responses to mixtures of compounds, which contributes to their flower visiting preferences and foraging behavior [22].

• Flower traits in a community context

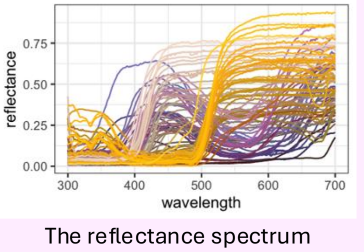
The diversity of flower chemical traits can be partially explained by the need of plants for attracting a subset of pollinators while discouraging others [11, 23]. Indeed, not all pollinators are equally effective for all plant species, while providing floral resources is energetically costly for plants.

Display traits

Color



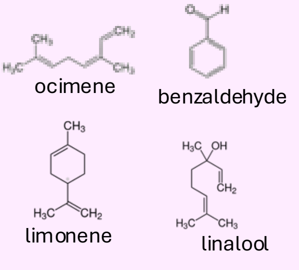
The high diversity of colors in an alpine grassland during summer.



The reflectance spectrum (proportion of light reflected across wavelengths) of flowers from 90 species from Calanda, Switzerland.

Scent

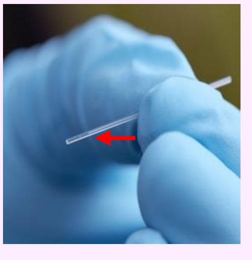
Collection of volatile compounds with a passive adsorption method [82].



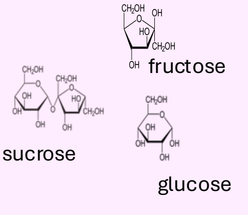
Floral volatile organic compounds are highly diverse (Examples shown).

Reward traits

Nectar

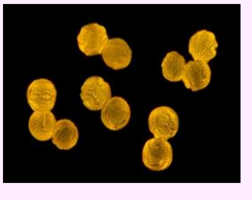


Collection of nectar into a microcapillary from individual flowers.

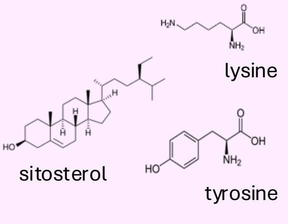


The main sugars in nectar are sucrose, glucose and fructose.

Pollen



Pollen grains of Taraxacum officinale, seen on an optical microscope.



Several important nutrients, such as lipids and amino acids, are present in pollen.

Figure 1: The main flower chemical traits can be categorised as display traits (color, scent) and reward traits (nectar and pollen composition)

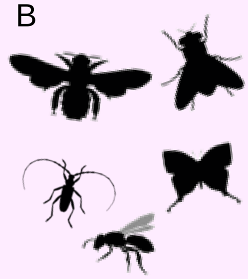


Figure 2: Plant and insect life in alpine grasslands

Pollination in alpine grasslands

Alpine grasslands

Alpine grasslands are the vegetation structure found above the treeline. In the central Alps, its mean elevation varies roughly from an altitude of 1800 to 2000 m, approximately [24]. In this setting, the varied rock substrate, orography, and climatic conditions, as well as gradients within these factors, make a complex landscape of micro-environments in which many plants and other organisms thrive [25]. Indeed, alpine grasslands have a high degree of endemism [26] and are one of the hot-spots of biological diversity in Europe [27]. Alpine grasslands in Europe are largely managed ecosystems, where seasonal grazing by cattle keeps the vegetation short. Without the seasonal influence of cattle, ecological succession would mean much of the current species-rich grassland area replaced by forests. On the contrary, the intensification of traditional management (more grazing events per season) promotes the overabundance of only the most resistant plant species. In consequence, both abandonment and grazing intensification are the largest current threats to alpine biodiversity [28, 29, 30].

Pollination in the alps - plant perspective

Alpine plant species **(Figure 2A)** are characterized by their resistance to harsh conditions – including a brief growing season, extreme temperature regimes, variable snow cover during the year, strong wind and inclination effects, high solar radiation, among others [25]. In face of these factors, alpine plants are often short, sometimes growing in dense patches in the spaces where they find suitable conditions. Plants in this environment seem to rely more heavily in insects for their pollination than in the lowlands [31]. Alpine plants have lower rates of genetic auto-compatibility, and the proportion of biomass invested into flowers relative to vegetative tissues is extreme in comparison with lowland plants [25], likely reflecting a high importance of achieving sexual reproduction. Recent studies have found that flowers at high elevations tend to be less morphologically specialized [32, 33]. That is, they present accessible flowers for diverse pollinators, often having a radial symmetry and open shape. This trend may be adaptively significant, as plants at high elevation may need to make use of any pollinators available [34].

Pollination in the alps - insect perspective

Pollinating insects **(Figure 2B)** have a different representation than they do in the lowlands – at higher altitudes, flying insects are less abundant, and the environmental conditions favor some groups more than others. Pollinator communities above the tree line are characterized by a decreasing abundance of bees and beetles, especially above 1500 m, with flies showing a softer decline with elevation [35, 36]. Butterflies have not been found to show a clear elevation pattern [36]. These patterns result in a higher proportion of flies at high elevation [35, 36, 34, 37], likely aided by suitable larval environments (moist soils rich in organic matter) [34], and by their lower energetic requirements. Among bees, bumblebees represent a special case; although they become less abundant with altitude, they are not as dramatically affected as solitary bees. Bumblebees are physiologically less sensitive to cold environments and are still relatively abundant in the alpine vegetation [35, 36]. Matching the case of flower morphology, insects at high elevations seem to be more generalist in their interactions with flowers, tending to visit a higher number of plant species [38].

Pollination in the alps - chemical traits

Whether there are overall differences in chemical traits in flowers when comparing lowland and alpine plant communities is unclear, as this topic is understudied. There are reasons to expect that they may be different [**Figure 3**]:

i) Alpine plants are subject to specific abiotic conditions, which may promote activity in certain metabolic routes [39]. Because several of those metabolic routes are implicated in the synthesis of pigments and volatiles [40, 41], it is possible that abiotic factors associated with altitude have simultaneous effects on several flower chemical traits.

ii) Particular chemical traits can be linked to particular pollinators guilds [42, 43]. Indeed, experimental evolution tests have shown that some plant chemical traits can quickly change in response to different pollinator regimes [44]. Because insect pollinator communities at high elevation are different from the lowlands (e.g., higher proportion of flies and bumblebees), it is possible that plant traits at high elevations tend to optimise attraction towards the occurring pollinators [34].

iii) Finally, plants communities in the alps may be over-represented in some plant groups (for example, plants in the family Ericaceae). As a consequence of shared evolutionary history, closelyrelated plants are expected to also share other traits (e.g., flower color), which are not necessarily related to the traits that allow them to live in such environment.

Understanding the diversity of flower chemical traits and how they regulate pollinator interactions is crucial in alpine grasslands. This knowledge can support the conservation of alpine pollination networks, and may also enable more targeted conservation strategies **[Information Box 2].**

Picture: PA State College, USA

Abiotic factors

Changes in plant metabolism as a response to temperature, solar radiation, water stress, etc.

Picture: Mihael Simonič

Pollinator community

Plants may adapt their traits to the preferences of local pollinators.

Picture: Muriel Bendel

Picture: Heinz Staudacher

Shared evolutionary history

Closely related plants that are common in alpine environments (e.g., species in family Ericaceae, which are able to survive in poor high-montane soils [45]) are more likely to share other traits, such as petal color.

Figure 3. Some factors that can influence flower chemical traits in high altitudes

Information box 2: Conservation of pollination in the Alps

Current approach to insect conservation

Insect conservation traditionally focuses on the protection of suitable habitats, given that insects have a high reproductive output in adequate conditions. Historically, insect protection has been a by-product of the protection of land for either plant or mammal habitats. Only recently has attention been brought to the evaluation of habitats with potential relevance for insects [48]. Insect habitat quality in grasslands seems to be mostly determined by heterogeneity of vegetation structure and species, which is useful for nesting and thermoregulation [49, 50], the latter of which is especially relevant to face climatic extremes [51]. In the case of alpine grasslands, heterogeneity in the management seems to be a suitable strategy for conservation. This can be achieved by the spatial and temporal separation of grazing management – some areas being grazed more than others, and at different times of the season [28, 52]. The latter strategy seems especially well-suited for pollinators, as it allows a longer availability of floral resources [28]. Apart from quality of habitat, habitat size and connectivity also play a minor role in the continued survival of grassland insects [53, 54].

Conservation of pollination networks

Recent work has advocated for the conservation of interaction networks instead of individual species [55, 56]. Protecting networks has the advantages of promoting the stability of systems, as well as ecosystem processes and services. To facilitate the evaluation and comparison of networks, several metrics have been devised; such as connectance, nestedness, and modularity. Pollination networks often share structural features as described by these metrics [57]. For example:

- Connectance (the proportion of all potential interactions actually occurring) is highly uneven for elements in pollination networks **(Figure 4A)**. Although the total connectance tends to be low , plants tend to have a higher connectance that pollinators, hinting at a higher priority for plants in conservation efforts. Connectance among insects is also highly unequal, with some better described as generalists and others as specialists.
- Networks are nested: Generalist pollinators visit a large proportion of plant species, while specialist pollinators only visit few, which are often also visited by generalists **(Figure 4B)**. This pattern can seem to be redundant. Yet, redundancy in interaction networks provides stability to disturbances.
- Networks present modules: Groups of plants have a tendency to interact more strongly with some groups of insects **(Figure 4C)**. This can happen if the plant traits are suitable for some insects, and less so for others. If some species have a higher conservation priority, identifying modules can provide a starting point for a more targeted approach.

Empirical examples of network-informed pollinator conservation practices are starting to emerge [58, 59, 60]. For example, a recent study on North American flatland grasslands highlighted the role of generalist pollinators in the stability of interaction networks across several years. Thus, in that system, the protection of generalists can be valuable in face of perturbations and climate change, likely benefiting rarer pollinator species [83]. A few studies have focused on alpine grasslands. For example, a recent study has revealed important pollinator species in an alpine system, for entire pollination networks and within phenological modules [60]. . However, a limitation of network-based approaches is the lack of integration with species-trait data. Indeed, integrating floral chemical traits can provide a predictive framework to pollination networks, which can better inform conservation and restorations practices [61].

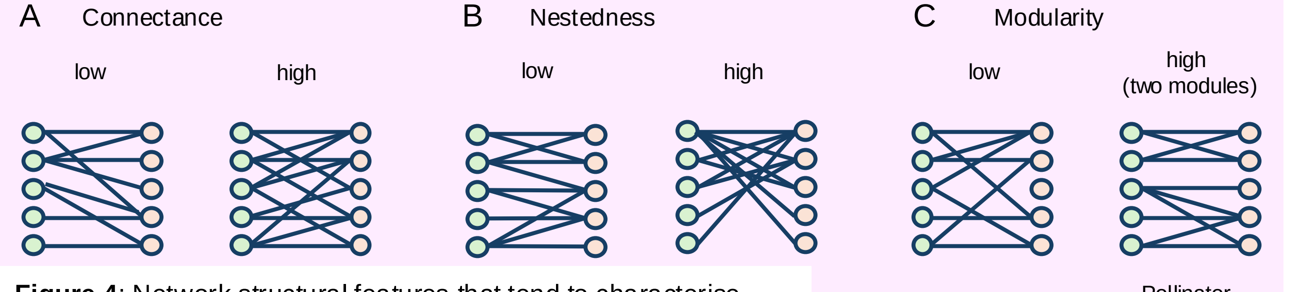


Figure 4: Network structural features that tend to characterise pollination networks (see text).

Case study: Calanda alpine grasslands

As original research conducted by the Information Ecology Zu group at ETH Zürich, we are currently studying the chemical traits that flowers possess in alpine grasslands. Further, we explore the associations among multiple types of flower traits (e.g., color and scent). Finally, we evaluate the link between the chemical traits and the network of interaction between plants and pollinators. The study is being conducted in two sites characterised as alpine grasslands, at an elevation of 1400 and 2000 meters, in Calanda, Switzerland.

Case study: Reward traits

The chemical composition of nectar is one of the traits that we are interested in. We tested whether the concentration of individual components in nectar was different between the two plant communities considered (in total 43 plant species). Preliminarily, we found that the concentration of the main sugars (sucrose, glucose, fructose) was not different between the two elevations. However, the proportion of sucrose among the main sugars was higher in the lower elevation **(Figure 6)**. This result may be related to a different pollinator community across elevations (higher proportion of sucrose has been related to flowers being more specialised in the type of pollinators they attract [46]), or to abiotic factors (higher sucrose has been linked to higher temperatures and lower water availability [47], both of which characterize our lower study site). Evidence of a potential link to pollinators comes from the relationship between sucrose concentration in nectar and visits by pollinator groups, particularly bees (**Figure 7**). Bees are often linked to higher sucrose concentration [46], and were more abundant in our lower site (**Figure 5**). Non-flower-specialist flies in contrast are linked to lower sucrose [46], and were more abundant in the higher site (**Figure 5**). Preliminary analysis detected a contrasting concentration of a few other metabolites between elevations. The potential role of those compounds is currently under investigation. Overall, our results hint that some nectar traits are different across elevation and suggest potential functional links to the pollinator community.

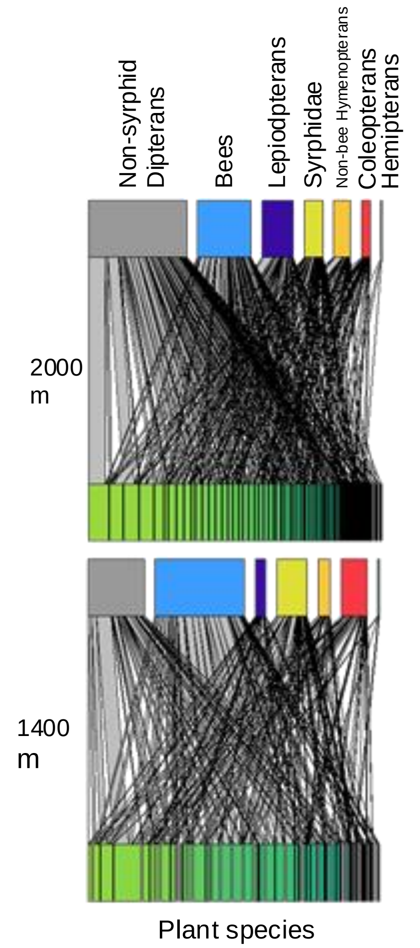
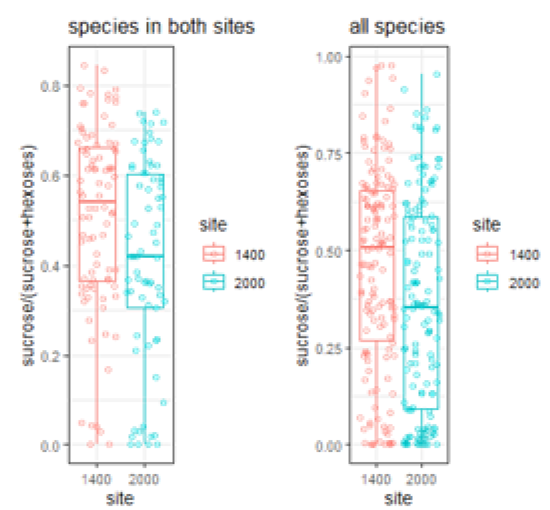


Figure 5. Networks of flower visitation by insect groups at the two sites in Calanda



Linear mixed-effects model, estimate -0.036, p = 0.0531

Linear mixed-effects model, estimate -0.044, p = 0.0431

Figure 6. Proportion of sucrose among the main sugars in nectar of alpine species, at two elevations.

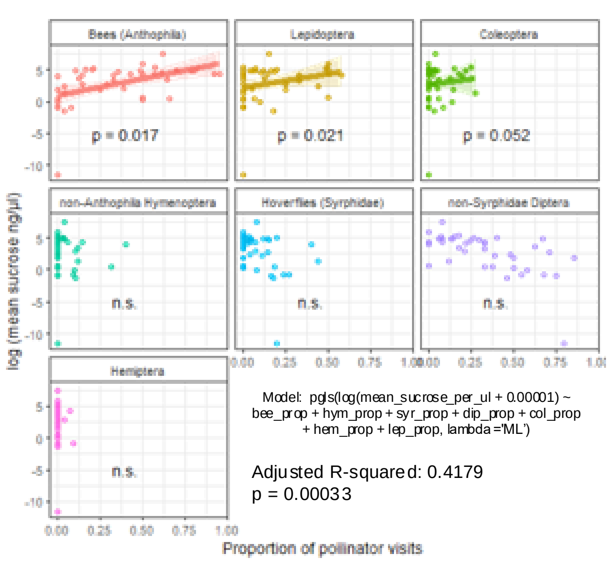


Figure 7. Relationship between the concentration of sucrose concentration in nectar (log scale) in flower nectar, and the proportion of visits by pollinator groups. The statistical test considers the phylogenetic relationship of plant species as a covariate.

Case study: Display traits

We are interested in the flower color in alpine plant communities. Specifically, we tested whether co-flowering plant communities have higher color diversity than expected by chance, and which biotic and abiotic factors are linked to the community color diversity. We evaluated these questions by incorporating flower spectral data (color), phytosociology, phenology, and abiotic traits, as well as models for insect color vision. Preliminary results showed that some co-flowering communities have a higher color diversity than expected by chance, while others have lower diversity. This diversity is dependent on the phenology of plant communities (**Figure 8**). Additionally, we found that within some communities, flowers with more contrasting colors have a more contrasting composition of associated pollinators. In separate tests, some color components were also found to be associated to visits by certain pollinator groups.

Overall, our preliminary results suggest that insect pollinators may play a role not only in shaping the color of individual flower species, but also in shaping the diversity of colors in some alpine co-flowering communities. Another preliminary finding is that delimiting plant co-flowering communities with both phytosociological and phenological characteristics is a promising approach for yielding insights into the community-level patterns of flower traits.

Case study: Conclusions and outlook

The chemical traits of flowers strongly shape their interactions with insect pollinators. Integrating trait-based data to interaction networks is a promising approach to design more targeted conservation practices, yet their application is only slowly emerging. Through our case study based in the Calanda grasslands, we aim to generate inisghts into the key traits and pollinator groups in maintaing the structure of pollination networks.

Ongoing work involves the detailed characterization of other flower chemical traits (pollen, scent) and the identification of insect specimens for constructing a high-resolution interaction network. Together with the Office for Nature and Environment of Grisons, we are committed to evaluating the implications of this research, and translating them into updated management practices for alpine biodiversity conservation. This knowledge can be useful for the protection of alpine grasslands as systems, as well as for the protection of listed threatened and endangered species.

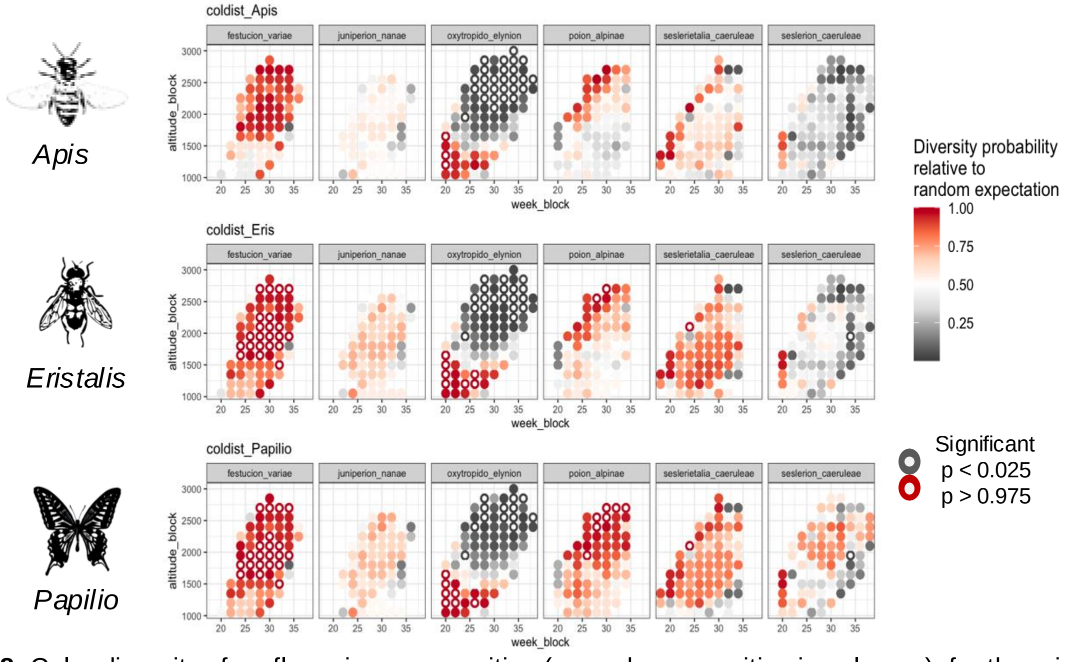


Figure 8. Color diversity of co-flowering communities (named communities in columns), for three insect color visual models (in rows). Each co-flowering plant community is represented by a data point in each panel, as estimated at a given altitude (y axis in panel), and a week of the year (x axis). The color represents the probability of the color diversity of the co-flowering community when contrasted against a null expectation model (distribution built by random sampling 1000 times from complete species dataset). A higer color diversity than expected by chance is represented in red, while a lower diversity in gray. A white circle represents if the color diversity in the co-flowering community reaches the significance threshold. (in the top or bottom 2.5% of the distribution).

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