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RESEARCH ARTICLE

Handbook of protocols for standardized measurements of floral traits for pollinators in temperate communities

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Abstract

1. Floral traits describe organs or structures directly related to plant reproduction, and they are essential to understanding plant–pollinator interactions, notably for conservation purposes.
2. The growth of plant trait-based approaches lies in the availability of data shared by the international research community on dedicated platforms, as well as in protocols compiled in handbooks on how to measure these traits in a standardized way. Floral traits are important pieces that are missing from these handbooks, likely due to the complexity of flower morphology.
3. Here, we present a handbook of standardized protocols dedicated to floral traits that can be applied to a wide set of temperate plant species to quantify these traits at the scale of plant communities. The 24 floral traits are grouped into three categories: visual and olfactory cues, accessibility and resources. We also provide four additional features related to flower abundance and phenology that we recommend measuring to scale up individual species' trait values to overall plant communities.
4. By collecting these floral traits in a standardized way, we promote applications in the context of community ecology to predict the diversity of pollinator communities, identify the effects of environmental changes and study plant–pollinator networks.

KEYWORDS
cues, floral resource, functional traits, nectar, network, phenology, pollen, pollination

1 | INTRODUCTION

Decades of research in ecology have been devoted to studying the links between the assembly of biodiversity and its effects on ecosystem functioning and, ultimately, the provision of ecosystem services (Cardinale et al., 2012; Harrison et al., 2014; Tilman et al., 2014). Awareness is increasing that ecosystem functioning is mediated not only by the number and composition of species but also by the functional traits within a community (Gagic et al., 2015; Hooper et al., 2005). This recognition, together with evidence that the functional composition of communities reflects the output of biotic and abiotic mechanisms, has motivated the use of functional trait-based approaches, which are well developed, particularly for plant species (e.g. McGill et al., 2006). Functional traits are defined as morphological, physiological and phenological features of individuals that impact fitness indirectly via their effects on growth, reproduction and survival (Violle et al., 2007). Moving from a taxonomic to a functional trait approach deepens the understanding of the distribution of organisms along environmental gradients (e.g. Chapin et al., 1993; Westoby et al., 2002), the coexistence of species within a community (e.g. Götzenberger et al., 2012; McGill et al., 2006) and the links between organism functioning and ecosystem services (Garnier & Navas, 2013; Lavorel & Garnier, 2002; Suding et al., 2008) allowing generalizations beyond specific taxa and regions. Trait-based ecology has historically been led by plant ecologists (e.g. Grime, 1979). The plant functional traits studied most are those described by Westoby (1998): specific leaf area (i.e. the ratio of leaf area to leaf dry mass), plant height and seed mass, which describe three axes of plant variation related to their resource management, competitive ability and regenerative capacity, respectively. The success of the plant trait approach is based on the availability of data but also on the existence of practical 'handbooks' that describe how plant traits should be quantified in a standardized way (Cornelissen et al., 2003), with one protocol selected per trait. Protocols have been standardized to use similar trait measurements across a range of species and limit experimental bias and environmental effects on trait values (e.g. Moretti et al., 2017). These protocols have been extended to other plant structures, such as modularity traits (Klimešová et al., 2019), wood (Chave et al., 2009) and roots (Guerrero-Ramírez et al., 2021), or several taxonomic groups, such as terrestrial invertebrates (Moretti et al., 2017). Standardization of trait measurements has undoubtedly facilitated the creation of large online databases containing many functional trait values for plants such as LEDA (Kleyer et al., 2008) and TRY (Kattge et al., 2020) which have helped develop comparative ecology analyses of ecosystems and even biomes (e.g. Scheiter et al., 2024).

Among functional traits, floral traits describe organs or structures directly related to plant reproduction. They play a key role in pollination ecology by driving flower attractiveness and accessibility to pollinators. Despite their central position among plant traits, floral traits are not included in handbooks for field studies of plant traits (Pérez-Harguindeguy et al., 2013). This is likely due to the great diversity of floral morphologies found in nature, classified as blossom types (Faegri & van der Pijl, 1979), whose traits are difficult to measure in a standardized way. Moreover, floral trait data are often incomplete in plant functional trait databases (E-Vojtkó et al., 2020), even though a floral trait-based approach is essential to determine relationships among floral traits at the plant scale (Roddy et al., 2021) and understand plant–pollinator interactions at macroecological scales. While classic network approaches based on taxonomy identify specific plant–pollinator interactions, a functional approach would focus on the diversity of plant characteristics that are essential for attracting pollinators with different traits and allow generalizations beyond specific taxa. In this context, floral traits shape matching between plants and pollinators (Lavorel et al., 2013), which determines the resulting pollination function at the community level. Pollination of ca. 87% of flowering plant species (Ollerton et al., 2011) and ca. 75% of crop plants (Klein et al., 2007) depends in part on plant–pollinator interactions. A better knowledge of the floral traits of different plant species is therefore a major challenge to understanding how these plant–pollinator interactions respond to changes in environmental factors and to better design our ecosystems to conserve pollinators. The scarcity of floral resources resulting from habitat loss and pesticide exposure is often cited as one of the main causes of pollinator decline (Goulson et al., 2015; Potts et al., 2010; Roulston & Goodell, 2011). Although pollinators need floral resources to survive, nectar and pollen quantity and quality have been little quantified because they are difficult to measure and respond to their environment in a highly variable manner (Junker & Parachnowitsch, 2015). One current challenge in pollination ecology is to quantify floral trait values in the field for a wide range of species and consider them at the community or even landscape scale. To date, only a few freely accessible datasets of quantitative floral traits, including floral rewards, are available (Baden-Böhm et al., 2022; Baude et al., 2016; Filipiak et al., 2022; Lanuza et al., 2023; Tew et al., 2023). The number of plant species included in these floral trait datasets (e.g. 1612 species in Filipiak et al., 2022; 1506 species in Lanuza et al., 2023 for the most comprehensive databases) is far lower than that in functional trait databases, which predominantly focus on vegetative traits, such as TRY (Kattge et al., 2020) which contains more than 300,000 species. This quantification of species' floral traits is based on the concept of comparative ecology already used in functional trait-based approaches. A handbook dedicated to floral traits would be valuable for scientists measuring quantitative values for many plant species in situ for a variety of reasons.

First, the pioneering literature on methods for pollination studies is rich (Dafni, 1992; Dafni et al., 2005; Faegri & van der Pijl, 1979; Kearns & Inouye, 1993; Knuth, 1906; Kugler, 1970). A large number of detailed protocols are precisely described in these books with information on the advantages and disadvantages of each method, but they can be complex for non-specialists to appropriate them. Studies at the community scale require applying rapid in situ protocols to many species at once. Moreover, enriching trait databases with data obtained from shared standardized protocols would be valuable for the scientific community to obtain mean trait values and/or make comparisons. Thus, we recommend a set of selected practical protocols appropriate for field community studies. This handbook of floral traits is based on existing practical guides for pollination ecology but considers advances in the conceptual framework of functional ecology and in analytical tools (especially chemical analysis). It therefore addresses various fields of research, including biology, agroecology, urban ecology, pollination ecology and conservation ecology; it is intended both for flower specialists and for those who are not but aspire to weave this perspective into their work.

Then, quantitative values for floral traits are necessary. Originally, flowers were categorized based on qualitative descriptions of certain traits, such as flower morphology, scent and reward in pollination syndromes (Faegri & van der Pijl, 1979; Fenster et al., 2004), and this last concept provides a hypothesis to explain floral evolution through adaptation to pollinators (Ollerton et al., 2009). Floral traits exhibited by plants may thus reflect phenotypic floral convergence adapted to pollination by functional groups of pollinators (e.g. bees, birds, butterflies). Many studies have used this categorization for plant–pollinator networks (Kingston & Mc Quillan, 2000; Ollerton et al., 2009; Rosas-Guerrero et al., 2014), although the concept of pollination syndromes is still debated (Ollerton et al., 2009; Rosas-Guerrero et al., 2014; Waser & Ollerton, 2006). As Dellinger (2020) highlighted, pollination syndrome studies have resulted mainly in considering only a few traits and qualitative rather than quantitative values for these traits.

Finally, compiling floral trait data requires minimizing data heterogeneity by standardizing the protocols. First, floral traits are not always well defined, which leads to misunderstanding about what exactly should be measured. This can also lead to combining values for different measurements under the same trait name. For example, the generic term 'flower size' can cover a wide range of distinct parameters that are measured differently, such as floral diameter, corolla size and floral planar projection (Dafni et al., 2005). Second, the literature often provides different protocols for measuring the same trait, which strongly influences the data obtained. For example, measurements of nectar volume depend greatly on the intensity of insect foraging. If a net that prevents insects from accessing the flowers for a given period is not set up, measurements of nectar quantity are no longer comparable. Thus, quantitative floral trait values may depend on the method applied, the context and the plant species.

Consequently, we developed a handbook of standardized protocols for 24 floral traits (Table 1) grouped into three main categories: visual and olfactory cues (i.e. floral area, flower size, floral height, floral reflectance and profile of volatile organic compound (VOC) emissions), accessibility (i.e. floral longevity, nectar tube depth and width, anther exertion) and resources (i.e. nectar volume, nectar sugar concentration, nectar sugar content, nectar sugar composition, nectar amino acid composition, nectar phenolic composition, nectar alkaloid composition, pollen grain number, pollen grain size, pollen volume, pollen protein composition, pollen polypeptide composition, pollen amino acid composition, pollen lipid composition, pollen sterol composition and pollen alkaloid composition). We chose to describe these 24 traits that we considered to be « matching traits » (i.e. traits mediate relationships between plants and pollinators) with the possibility to scale them at the community level. The traits were grouped by the main category to which they belong, but the categories may not be exclusive. For example, floral area was considered a visual and olfactory cue, but it influences the accessibility of floral units (FUs) to pollinators. In addition, we provide preliminary considerations of the definition of FUs (Table 2) and the four additional features (i.e. floral density, floral density per unit of vegetation cover, floral cover and flowering phenology) (Table 3) that we recommend measuring to scale up individual species' trait values to overall plant communities. Although not explicitly specified in each trait description, both biotic and abiotic conditions can modify floral trait values. We limited this handbook to temperate ecosystems because of the many unique characteristics of pollination in tropical ecosystems.

2 | METHODOLOGY

2.1 | Handbook compilation

To develop this handbook, scientists from pollination ecology, community ecology, functional ecology and chemical ecology of plant–pollinator interactions joined a working group of the French, Belgian and Swiss research group 'Pollineco,' which studies 'Pollination, ecological networks and ecosystem functioning' (GDR Pollineco, 2023). The main objectives of this working group were (1) to select and define the floral traits of ecological importance in the context of plant–pollinator interactions. Consequently, this handbook excludes certain floral traits (in particular, those related to flower construction costs or reproductive systems) (2) to produce a series of easy-to-use protocols for floral traits that can be applied to a variety of plant species regardless of their floral type from a community-wide perspective and (3) to discuss, find compromises for and approve the handbook's recommendations, such as the unit used or the sampling effort. In a second step, researchers from other countries helped to complete this handbook using common and mutually accepted protocols. The protocols can be innovative when they benefit from recent technological advances, or they can be easy-to-use existing protocols commonly shared by users. Like existing handbooks (e.g. Cornelissen et al., 2003; Klimešová et al., 2019; Moretti et al., 2017),

TABLE 1 Main category, definitions and scale of measurement of the 24 floral traits considered in this handbook.

Main category	Floral trait	Definition	Scale of measurement
Visual and olfactory cues	Floral area	Area of the largest visible surface of the FU, considered to have a rectangular or circular shape depending on the species	FU
	Flower size	Flattened projected surface of all petals of the flower	Flower
	Floral height	Shortest distance between the top FU of an individual and the ground	FU
	Floral reflectance	Wavelength-specific proportion of light reflected by the FU (usually measured in regular wavelength intervals, such as every 1 nm)	FU
	Profile of volatile organic compounds	Quantities or semi-quantities of multiple VOCs emitted around a plant (i.e. its headspace)	FU
Accessibility	Floral longevity	Duration that the flower remains open in the field and functionally active	Flower
	Flower depth and width	Distance from the flower's opening to its base, while flower width is measured at the middle of the flower	Flower
	Anther exsertion	Distance between the centre of anthers and points on the plane formed by the flower opening	Flower
Resources	Nectar volume	Volume of nectar produced per flower after 24 h of bagging	Flower
	Nectar sugar concentration	Sugar concentration in nectar produced per flower after 24 h of bagging	Flower
	Nectar sugar content	Quantity of sugar in nectar produced per flower after 24 h of bagging, calculated from measurements of nectar volume and sugar concentration	Flower
	Nectar sugar composition	Concentration of each sugar in nectar	Sample
	Nectar amino acid composition	Concentration of each amino acid in nectar	Sample
	Nectar phenolic composition	Concentration of each phenol in nectar	Sample
	Nectar alkaloid composition	Concentration of each alkaloid in nectar	Sample
	Pollen grain number	Number of pollen grains produced per flower	Flower
	Pollen grain size	Volume of one pollen grain	Sample
	Total pollen volume	Total volume that pollen grains occupy per flower	Flower
	Total pollen protein concentration	Concentration of total proteins in pollen	Sample
	Pollen polypeptide composition	Concentration of each polypeptide in pollen	Sample
	Pollen amino acid composition	Concentration of each amino acid in pollen	Sample
	Pollen lipid composition	Concentration of each lipid in pollen	Sample
	Pollen sterol composition	Concentration of each sterol in pollen	Sample
	Pollen alkaloid composition	Concentration of each alkaloid in pollen	Sample

Note: A floral unit (FU) is usually defined as one or more flowers that can be visited by a pollinator walking without the need to fly when foraging (see Appendix S1 for more details).

this handbook provides for each trait a brief ecological introduction, a standardized protocol for measuring traits, special cases and associated references. All protocols for 24 floral traits and four additional features are provided in Appendix S1.

2.2 | Recommendations for standardization

We have identified three stages for the standardization of floral trait measurements in terms of sample collection, protocols and data, respectively. We first recommend selecting flowers from well-grown plants with a healthy appearance and no signs of pathogens or extensive herbivory. The phenology of individual flowers can be divided into several stages. About 85% of angiosperms (Barrett, 1998; Lloyd & Webb, 1986) are dichogamous, meaning that their male and female reproductive organs mature at different times during the reproductive phase. Dichogamy may exist in a single hermaphrodite flower or among flowers in dioecious or monoecious species (Lloyd & Webb, 1986). The two modalities of dichogamy are protandry, where the male phase precedes the female phase, and protogyny, where the pattern is reversed. Dichogamy generally acts as a mechanism to increase the rate of cross-fertilization (Barrett, 1998). For

TABLE 2 Floral unit types and examples of corresponding plant taxa reported by Baldock et al. (2015) and Casanelles-Abella et al. (2021).

Floral unit type	Plant taxa reported by Baldock et al. (2015)	Plant taxa reported by Casanelles-Abella et al. (2021)
Single flower	*Alstroemeria* spp., all Amaranthaceae, *Allium* spp., *Vinca* spp., *Ilex* spp., *Zantedeschia* spp., *Hedera* spp., *Hyacinthoides* spp., *Impatiens* spp., *Berberis* spp., *Mahonia* spp., all Boraginaceae, all Brassicaceae, all Campanulaceae, all Caprifoliaceae (except for *Sambucus* spp.), all Caryophyllaceae, *Euonymus* spp., all Cistaceae, all Convolvulaceae, *Sedum* spp., *Dipsacus fullonum*, *Elaeagnus* spp., all Ericaceae (except for *Calluna vulgaris*), *Escallonia* spp., all Fabaceae (except for *Medicago* spp. and *Trifolium* spp.), all Fumariaceae, all Geraniaceae, *Hydrangea* spp., *Hypericum* spp., *Crocosmia* spp., all Lamiaceae (except for *Lavandula* spp.), *Laurus nobilis*, *Hemerocallis* spp., *Linum* spp., all Malvaceae, *Narthecium ossifragum*, all Oleaceae, all Onagraceae, all Orchidaceae, all Orobanchaceae, *Oxalis* spp., all Papaveraceae, *Mimulus* spp., *Plantago* spp., *Armeria* spp., *Phlox* spp., *Polygala* spp., all Polygonaceae, *Claytonia* spp., all Primulaceae, all Ranunculaceae, all Rosaceae (except for *Spiraea* spp. and *Prunus lusitanica*), all Rubiaceae, *Choisya* spp., all Scrophulariaceae (except for *Buddleja* spp.), *Veronica pimeleoides*, *Veronica* spp. (subgenus *Pseudoveronica*), *Veronica speciosa*, all Solanaceae, *Tropaeolum* spp., *Valerianella locusta*, *Viola* spp.	Acanthaceae, Alismataceae, Amaranthaceae, Anacardiaceae, Apocynaceae, Asparagaceae, Balsaminaceae, Begoniaceae, Boraginaceae, Brassicaceae, Campanulaceae (except *Phyteuma* spp.), Caprifoliaceae (except Dipsacoideae), Caryophyllaceae, Celastraceae, Cistaceae, Cleomaceae, Convolvulaceae, Crassulaceae, Cucurbitaceae, *Cytisus* spp., Geraniaceae, Hypericaceae, Iridaceae, Lamiaceae, *Lathyrus* spp., Linaceae, Lythraceae, Magnoliaceae, Malvaceae, Onagraceae, Orchidaceae, Orobanchaceae, Oxalidaceae, Papaveraceae, Phrymaceae, Plantaginaceae (except *Plantago* spp.), Polemoniaceae, Polygonaceae, Portulacaceae, Primulaceae, Ranunculaceae, Resedaceae, Rhododendron spp., Rosaceae (except *Filipendula ulmaria*, *Sanguisorba* spp., *Spiraea* spp.), Rutaceae, Saxifragaceae, Spartium spp., Solanaceae, Scrophulariaceae (except *Buddleja davidii*), Tropaeolaceae, Verbenaceae, Violaceae, Xanthorrhoeaceae
Single capitulum	All Asteraceae (except *Solidago canadensis*), *Knautia arvensis*	Asteraceae, Dipsacoideae
Single branch of capitula	*Solidago canadensis*	
Part of panicle	*Spiraea* spp. (except for *Spiraea douglasii*)	
Single umbel		*Allium* spp.
Secondary umbel	All Apiaceae	Apiaceae
Single compound cyme	All Valerianaceae (except for *Valerianella locusta*)	*Centranthus* spp.
Single corymb or single cyme	*Cornus* spp., *Sambucus* spp., *Euphorbia* spp.	Adoxaceae, Cornaceae, *Hydrangea* spp., *Euphorbia* spp.
Single panicle	*Buddleja* spp., *Spiraea douglasii*	Sapindaceae, *Buddleja davidii*, *Galium* spp., *Filipendula ulmaria*, *Sherardia arvensis*, *Spiraea* spp., *Syringa vulgaris*
Single raceme	*Calluna vulgaris*, *Medicago* spp., *Prunus lusitanica*, *Trifolium* spp., *Veronica pimeleoides*, *Veronica* spp. (subgenus *Pseudoveronica*), *Veronica speciosa*	Fabaceae (except *Cytisus* spp., *Lathyrus* spp., *Spartium* spp.), *Hedera helix*, *Ligustrum* spp., Vitaceae
Single spike	*Callistemon* spp., *Lavandula* spp.	*Plantago* spp., *Tamarix* spp.
Single thyrse	*Ceanothus* spp.	
Single dense cluster		*Sanguisorba* spp.
Single catkin		Betulaceae, Fagaceae, Salicaceae

Note: Floral unit types describe the scale (i.e. the part of the inflorescence) at which the trait measurements are to be made (except for the traits that are always measured at the flower scale, Table 1), depending on the species.

TABLE 3 Definition and scale of measurement of additional features used to aggregate species trait values to plant communities.

Feature	Definition	Scale of measurement
Floral density	Number of open flowers (or floral units) counted for each flowering species per unit of sampling area	Unit of the sampling area
Floral density per unit of vegetation cover	Number of open flowers (or floral units) counted for each floral species per unit of vegetation cover occupied by the species of interest	Unit of vegetation cover
Floral cover	Percentage of space occupied by each open floral species seen from above in the sampling area	Unit of the sampling area
Flowering phenology	Timing (e.g. onset, peak and end) of flower (or FU) production and duration of flower (or FU) production	Unit of the sampling area

example, for a protandrous hermaphrodite flower, six stages can be distinguished: (1) Flowers newly opened but not yielding pollen (immature staminate); (2) pollen present (mature staminate); (3) no pollen present, style elongating; (4) stigma exerted but not receptive (immature pistillate); (5) stigma receptive (mature pistillate); and (6) flower wilting (old pistillate) (Jacquemart et al., 2019; Vervoort et al., 2011). The flowers sampled should be in anthesis and receptive (i.e. stages 2–5) for most trait measurements except those in the resource category. To measure nectar quantity or composition, we recommend installing exclusion nets on young flowers (stages 1–4) to prevent them from wilting the following day and sugar content from varying among flower stages (e.g. Varga et al., 2013). To measure pollen quantity or composition, flowers should not have opened yet; we recommend collecting mature flower buds to facilitate the opening of flowers in the laboratory. For monoecious, dioecious, or other diclinous plant species (i.e. with reproductive systems that have unisexual flowers), we recommend stratifying the sampling between male and female flowers to estimate a representative mean per species. Flowers should be sampled from different plants and locations in the sampling area to ensure independence. We recommend measuring traits or collecting plant material on sunny days from 10:00 to 17:00, since all species except for night-flowering species close their flowers at the end of the afternoon. This sunny period corresponds to preferential foraging conditions for diurnal pollinators. Since most floral traits vary according to climatic conditions (e.g. temperature, humidity, light), we recommend sampling traits under preferential foraging conditions and recording all metadata on environmental conditions.

Second, for each trait measurement, we present a single easy-to-use protocol that can be applied to a variety of plant species from a community-wide perspective. We believe that implementing these unique protocols will help standardize measurement methods among different users. Since the reliability of a protocol lies in its reproducibility, we suggest the amount of material to sample and analytical replicates to make where appropriate, such as for the biochemical composition of nectar and pollen (see Table 4).

Third, for each floral trait and additional feature, we provide the recommended unit and examples of the range of observed values, according to current knowledge (Tables 4 and 5). We also estimate the time required to measure a sample and provide both minimum and recommended sample sizes to achieve a species-representative average for each trait, although few studies have investigated the intraspecific variability in floral traits (but see Kuppler et al. (2020), who studied the influence of abiotic and biotic factors on intraspecific variation in vegetative and floral traits at a global scale). The sample sizes are appropriate for comparative ecology based on differing trait values among species and for feasible collection in the field at the community scale. They need to be increased if the study objectives are to analyse (1) intraspecific variability in floral traits or (2) the response of floral traits to an environmental factor (i.e. response trait, as defined by Lavorel & Garnier, 2002). This information on the recommended unit, time required and sample size is essential to develop these trait measurements in various research fields.

2.3 | Metadata for floral traits

The standardized data acquired will need to be accompanied by some metadata, particularly in order to build databases and ensure their interoperability. The most important metadata include the location (i.e. GPS coordinates, city and country), habitat (for Europe, preferably the EUNIS classification), the date and hour, weather information (i.e. temperature, precipitation, cloud cover and wind speed), the name of the observer and contact details of the person responsible for the data. The nomenclature of plant species should follow international standards such as GBIF taxon ID (https://www.gbif.org), which is essential for the interoperability of databases. Information about the sampling protocol and measurements should also be included. In addition, specify the type of the FU (Table 2) on which traits were measured (i.e. single flowers or group of flowers, ideally with estimates of the number of flowers per FU). This information is crucial for analysing large-scale trends (see Appendix S1).

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TABLE 4 Recommendations for sampling the 24 floral traits included in the handbook. Traits are associated with preferred units and examples of ranges of values.

Floral trait	Preferred units	Example of value range	Recommended minimum sample size	Preferred sample size	Recommended material amount	Estimated time (per sample)
Floral area	mm^2	1–19,933 mm^2 (Michelot-Antalik, unpublished data)	5 floral units	10 floral units		<1 min
Flower size	mm^2	0.02–15.7 mm^2 (Genty et al., 2023)	5 flowers	10 flowers		3–8 min
Floral height	m	0.01–30 m (for plant height in Lanuza et al., 2023)	10 floral units	20 floral units		<1 min
Floral reflectance	No unit	0–1 (Arnold et al., 2010)	10 floral units and 10 leaves	20 floral units and 20 leaves		1–5 min
Profile of volatile organic compounds	ng (equivalent internal standard) $g^{-1} h^{-1}$	5–500 ng (equivalent internal standard) $g^{-1} h^{-1}$ (Kergunteuil and Proffit, pers. com.)	7 plants or floral units	12 plants or floral units		30 min to 4 h
Floral longevity	days	1–21 days (Ashman & Schoen, 1994)	10 flowers	20 flowers		1–5 min
Flower depth and width	mm	0–128 mm for depth and 0–9.5 mm for width (Baude, unpublished)	5 flowers	10 flowers		1–5 min (including dissection)
Anther exsertion	mm	−5.33 to +13.52 mm (Junker et al., 2013)	5 flowers	10 flowers		1–5 min
Nectar volume	µL per 24 h	0–55 µL (Baude, unpublished)	10 flowers	20 flowers		1–5 min
Nectar sugar concentration	°Brix sucrose (%)	0%–100% (Lanuza et al., 2023)	10 flowers	20 flowers	>0.1 µL	1 min
Nectar sugar content	µg of sugars per flower per 24 h	0–7768 µg (Baude et al., 2016)	10 flowers	20 flowers	>0.1 µL	1 min
Nectar sugar composition	$\mu g \mu L^{-1}$	0–118.9 $\mu g \mu L^{-1}$ (Venjakob et al., 2022)	5 samples	10 samples	1–10 µL	5–10 min
Nectar amino acid composition	$\mu g \mu L^{-1}$	0–15.1 $\mu g \mu L^{-1}$ (Venjakob et al., 2022)	5 samples	10 samples	1–10 µL	5–10 min
Nectar phenolic composition	$\mu g \mu L^{-1}$	0–1.99 $\mu g \mu L^{-1}$ (Palmer-Young et al., 2019)	5 samples	10 samples	1–10 µL	5–10 min
Nectar alkaloid composition	$\mu g \mu L^{-1}$	0–1.35 $\mu g \mu L^{-1}$ (Palmer-Young et al., 2019)	5 samples	10 samples	1–10 µL	5–10 min
Pollen grain number	Number of pollen grains per flower	13–2 × 10^8 (Lanuza et al., 2023)	5 samples	10 samples		2–4 h
Pollen grain size	μm^3	18–1.30 × 10^6 μm^3 (Baude et al., submitted)	5 grains	10 grains		1–5 min
Total pollen volume	mm^3 per flower	0.0003–20 mm^3 per flower (Baude et al., submitted)	5 samples	10 samples		2–4 h
Total pollen protein concentration	$\mu g\, mg^{-1}$	46.3–469.5 (Vaudo et al., 2024)	5 samples (×3 analytical replicates)	10 samples (×3 analytical replicates)	1–3 mg	48 h

(Continues)

TABLE 4 (Continued)

Floral trait	Preferred units	Example of value range	Recommended minimum sample size	Preferred sample size	Recommended material amount	Estimated time (per sample)
Pollen polypeptide composition	$\mu g\, mg^{-1}$	3.37–24.32 for total polypeptids (Vanderplanck et al., 2014)	5 samples (×3 analytical replicates)	10 samples (×3 analytical replicates)	5 mg	48 h
Pollen amino acid composition	$\mu g\, mg^{-1}$	0–70.4 $\mu g\, mg^{-1}$ (Jeannerod et al., 2022)	5 samples (×3 analytical replicates)	10 samples (×3 analytical replicates)	3 mg	48 h
Pollen lipid composition	$\mu g\, mg^{-1}$	10.2–190.0 $\mu g\, mg^{-1}$ for total lipids (Vaudo et al., 2024)	5 samples (×3 analytical replicates)	10 samples (×3 analytical replicates)	1 mg	48 h
Pollen sterol composition	$\mu g\, mg^{-1}$	0–90.9 $\mu g\, mg^{-1}$ (Zu et al., 2021)	5 samples (×3 analytical replicates)	10 samples (×3 analytical replicates)	20 mg	48 h
Pollen alkaloid composition	$\mu g\, mg^{-1}$	0–41.3 $\mu g\, mg^{-1}$ (Trunz et al., 2020)	5 samples (×3 analytical replicates)	10 samples (×3 analytical replicates)	1 mg	48 h

Note: Recommended sample sizes indicate the minimum and preferred number of individuals (i.e. flowers, floral units or samples) to sample depending on the trait. The recommended material amount indicates the quantity of resources required per sample for analytical analyses. The estimated time is that required for the measurement (or analysis), per sample.

3 | FUTURE APPLICATIONS AND PERSPECTIVES IN POLLINATION ECOLOGY

Based on these standardized protocols, we hope to encourage scientific cooperation to build a database of quantitative values for floral traits for a large number of species, with promising perspectives.

3.1 | Standardized floral traits to predict pollinator diversity of communities

First, collecting standardized quantitative floral trait data using the protocols in this handbook is useful for characterizing plant communities from a pollinator-related functional perspective. A local database is often the best way to estimate floral traits, which vary in space and time. Few such databases exist, however, and they represent a major sampling effort. When they are lacking, it is essential to have a database of mean floral traits per species from several locations to have quantitative data. Standardization then becomes a major issue to provide homogeneous and comparable data. By combining these data with vegetation surveys, trait-specific (or overall) functional indices, such as floral community-weighted mean or functional diversity, can be calculated and compared to pollinator-related variables (e.g. abundance, diversity, body size). These relationships and the processes that influence them remain little explored or understood. According to the mass ratio hypothesis (Grime, 1998; Hector, 1998), floral community-weighted means of visual cues would increase pollinator richness and abundance due to the dominance of certain floral traits. The mass ratio hypothesis has sometimes been supported (e.g. Fornoff et al., 2017) for plant–pollinator interactions, but mainly for means of floral traits of visited flowering species only (e.g. Hegland & Totland, 2005), not for all floral communities. The niche complementarity hypothesis states that higher floral functional diversity will be associated with more ecological niches, resulting in higher pollinator diversity and activity (Schleuning et al., 2015). This relationship between floral functional diversity and pollinator abundance has been observed to be positive (Goulnik et al., 2020; Junker et al., 2013, 2015) or negative (Fornoff et al., 2017; Uyttenbroeck et al., 2017) and seems to depend on habitats, local pools of plants and pollinators and the spatio-temporal scales considered.

Thus, collecting standardized floral trait data is essential in the context of pollinator conservation to establish a functional indicator of the pollination potential of various habitats. Currently, indicators of the pollination potential of land cover are based mainly on expert judgement at large spatial scales (e.g. Zulian et al., 2013) or on nectar or honey production of the species in plant communities (Baude et al., 2016; Desaegher et al., 2021). In a quantitative floral trait approach, a potential pollination score could be attributed to each plant species based on values for the traits they exhibited (e.g. phenology, visual and olfactory cues, accessibility, resources)

TABLE 5 Recommendations for sampling the additional features.

Floral trait	Preferred units	Example of value range	Minimum recommended sample size	Preferred sample size	Estimated time (per sample)
Floral density	Flowers or FU m^{-2}	132–21,700 flowers (Filipiak et al., 2022)	5 quadrats of 1 m^2	10 quadrats of 1 m^2	5–10 min m^{-2}
Floral density per unit of vegetation cover	Flowers or FU m^{-2} of vegetation cover	1–4 × 10^5 flowers (Baude et al., 2016)	5 quadrats of 1 m^2	10 quadrats of 1 m^2	5–10 min m^{-2}
Floral cover	%	0%–60%	5 quadrats of 1 m^2	10 quadrats of 1 m^2	1–5 min m^{-2}
Flowering phenology	Day of year of flowering start, end and peak Days for flower or FU duration	1–365 (Ecological Flora of Britain and Ireland, n.d.)	5 quadrats of 1 m^2	10 quadrats of 1 m^2	1–5 min m^{-2}

Note: Features are associated with preferred units and examples of ranges of values that can be encountered under field-grown conditions. Recommended sample sizes indicate the minimum and preferred number of sampling areas (i.e. quadrats) to install depending on the trait. The estimated time is that required for the measurement, per sample.

Abbreviation: FU, floral unit.

and their potential attractiveness to different pollinator taxa (Ricou et al., 2014). This functional indicator could then be used to refine the pollination potential of various habitats.

Beyond a taxonomic approach, this functional view of flora can be transferred to stakeholders to favour species or communities of plants that are more attractive and nutritious for pollinators and also to maintain the pollination service. Managing these floral resources at the landscape scale could conserve pollinators, particularly in environments in which they are prone to decline.

3.2 | Standardized floral traits as response traits to environmental changes

This handbook is a starting point for measuring floral response traits and studying relationships between environmental factors and plant–pollinator interactions. Doing so may require taking more samples than the number we recommended in order to represent the variability in these responses. The literature provides several examples of response traits, but a more detailed selection of these traits and their environmental drivers is needed. For example, environmental conditions (e.g. temperature, precipitation, concentrations of atmospheric pollutants and ultraviolet radiation) are expected to influence emissions of VOCs, which have been extensively studied for leaves (Peñuelas & Staudt, 2010) but much less for flowers (Farré-Armengol et al., 2013). In the context of climate change, there is an urgent need to study the effects of drought and water stress on floral traits, especially those related to visual and olfactory cues and resources. These floral traits can respond differently (e.g. Quinanzoni et al., 2024; see Descamps et al., 2021; Kuppler & Kotowska, 2021 for a recent review and meta-analysis), and these effects can decrease the number of pollinator visits (Descamps et al., 2021) and thus pollination. Climate warming could also induce morphological plant–pollinator mismatches between the flowering period and pollinator emergence (e.g. Hegland et al., 2009; Hutchings et al., 2018). Moreover, recent studies highlight the effects of drought on the composition and quantity of VOCs (Burkle & Runyon, 2016; Jaworski et al., 2022).

Another example of a major environmental factor is the response of floral traits to agricultural intensification in grasslands (i.e. the intensity of agricultural practices, such as mowing, grazing and fertilization; see Goulnik et al. (2021)). Agricultural intensification can change plant composition and thus modify flower colour (Binkenstein et al., 2013), decrease the mean nectar tube depth (Kühsel & Blüthgen, 2015), decrease reward production (Baude et al., 2016) and pollen quality (Kühsel & Blüthgen, 2015) or increase reward production for Mediterranean weeds at the scale of a plant community (Genty et al., 2025). However, the effects of intensification on floral scents and floral reward quality have rarely been studied.

3.3 | Standardized floral traits for plant–pollinator networks

Standardizing floral traits could be valuable for studying trait matching, which is one of several mechanisms (reviewed in Vázquez et al., 2009) that explain the structure of plant–pollinator networks (Rezende et al., 2007; Stang et al., 2007). Trait matching lies mainly in the match between flowers and pollinators' traits, thus acting as a floral filter for certain pollinators. For example, the match between flowering phenology and the flight period of insects determines, before anything else, whether an interaction can be established (Junker et al., 2013; Peralta et al., 2020; Vázquez et al., 2009). Morphological constraints such as the depth of the nectar tube in relation to the length of pollinator mouthparts lead to exploitation barriers (Stang et al., 2006, 2007; van Rijn & Wäckers, 2016).

Also, because it deters some pollinators, floral scent and other chemical traits can also contribute to network structure (Junker & Blüthgen, 2010; Kessler et al., 2008; Larue et al., 2016; Raguso, 2008). Due to the lack of quantified nectar and pollen data (as revealed by the compilation of traits in the literature by Lanuza et al. (2023)), almost no studies of reward-related traits or pollinator traits (e.g. body mass, body size, mouthpart/tongue length) exist, despite their importance for understanding pollinator niche occupancy. By standardizing the measurements of quantitative floral traits, trait matching could be addressed using a comprehensive multi-trait approach at macro-ecological scales, but it is not currently being studied (but see the recent study by Lanuza et al., 2023).

4 | CONCLUSIONS

This handbook is the result of a collective effort to provide standardized protocols for floral traits that are generally lacking for field experiments for many species and are often incomplete in plant functional trait databases. We recommend that a wide variety of researchers use this handbook to facilitate measurements, enable comparisons and render them spatially explicit at large scales, from communities to landscapes. These collected data can be placed into functional open databases such as TRY, national taxonomic repositories or new specific databases that relate floral traits and pollinators. We highlight three applications. First, floral traits can be used to build functional indicators of plant communities and manage more attractive and nutritious landscapes for flower-visiting insects. Increased functional floral diversity could also help regulate ecosystem services such as pollination and natural pest regulation in the context of agroecological transition or improve floral management to conserve biodiversity in urban areas. Second, standardized floral trait measurements are useful for understanding mechanistic responses of plant–pollinator interactions to changes in environmental factors. The response traits identified could then be used as proxies of plant–pollinator responses to environmental changes. Third, using floral traits in plant–pollinator networks can improve understanding of plant–pollinator matching at macro-ecological scales. Some plant species with specific floral trait values could be identified as essential to conserve specialist pollinators. This handbook could therefore provide many other perspectives, both for fundamental knowledge and practical applications in biodiversity conservation and management of human-impacted environments.

AUTHOR CONTRIBUTIONS

Alice Michelot-Antalik and Mathilde Baude conceived the ideas, organized the manuscript writing and wrote the first version of the Introduction and Discussion. Several groups of authors wrote sections for the floral traits: Mathilde Baude, Jérémy Goulnik, Alban Langlois and Alice Michelot-Antalik for 'floral area'; Mathilde Baude, Léa Genty and Alice Michelot-Anatalik for 'flower size'; Mathilde Baude, Alban Langlois and Alice Michelot-Antalik for 'flower height'; Jérémy Goulnik, Robert R. Junker, Alice Michelot-Antalik, Bertrand Schatz and Anna E- Vojtko for 'floral reflectance'; Alan Kergunteuil, Alice Michelot-Antalik and Magali Proffit for 'profile of volatile organic components'; Mathilde Baude, Anne-Laure Jacquemart and Alice Michelot-Antalik for 'flower longevity'; Mathilde Baude, Jérémy Goulnik, Alban Langlois and Alice Michelot-Antalik for 'flower depth and width'; James Desaegher and Mathilde Baude for 'anther exertion'; Mathilde Baude, Anne-Laure Jacquemart, Alban Langlois and Alice Michelot-Antalik for 'nectar volume, concentration and sugar content'; Jérémy Grosjean, Anne-Laure Jacquemart, Léna Jeannerod, Alice Michelot-Antalik and Maryse Vanderplank for all traits related to 'nectar composition'; Mathilde Baude, Alban Langlois and Jean-François Odoux for 'pollen grain number', 'pollen grain size' and 'total pollen volume'; and Anne-Laure Jacquemart, Léna Jeannerod and Maryse Vanderplank for all traits related to 'pollen composition'. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

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No data are associated with this manuscript.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1: Traits protocols.

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