Viewpoints

Towards the flower economics spectrum

Summary

Understanding how floral traits affect reproduction is key for understanding genetic diversity, speciation, and trait evolution in the face of global changes and pollinator decline. However, there has not yet been a unified framework to characterize the major trade-offs and axes of floral trait variation. Here, we propose the development of a floral economics spectrum (FES) that incorporates the multiple pathways by which floral traits can be shaped by multiple agents of selection acting on multiple flower functions. For example, while pollinator-mediated selection has been considered the primary factor affecting flower evolution, selection by nonpollinator agents can reinforce or oppose pollinator selection, and, therefore, affect floral trait variation. In addition to pollinators, the FES should consider nonpollinator biotic agents and floral physiological costs, broadening the drivers of floral traits beyond pollinators. We discuss how coordinated evolution and trade-offs among floral traits and between floral and vegetative traits may influence the distribution of floral traits across biomes and lineages, thereby influencing organismal evolution and community assembly.

While most studies of the selective agents acting on flowers are often focused on narrow taxonomic groups, understanding the relative contributions of different selective agents requires a comparative approach that employs standardised trait measurements applicable to many species. Here we propose the flower economics spectrum (FES), which can be used to identify axes of floral trait covariation and to assess whether there are central trade-offs in the construction and function of flowers and floral organs. Comparing the FES with the leaf economics spectrum will help distinguish the features of both that are shaped by fundamental trade-offs and those that represent the effects of selection eliminating certain trait combinations (Roddy et al., 2019). As a first step towards building the FES, we focus on the showy perianth structures, but we expect that similar axes of trait variation may also apply to other floral organs and to nonbiotically pollinated species. To provide the basis for such an understanding, we discuss the multiple agents of selection acting on flowers and the differences in the functional ecology of leaves and flowers. We then provide examples of specific predictions that could be tested using the FES. Finally, we argue that a

framework addressing the simultaneous roles of pollinators, enemies, and environmental factors acting on floral traits would enable us to identify major trade-offs and adaptations that shape floral diversity globally, just as leaf (Wright et al., 2004; Donovan et al., 2011), wood (Chave et al., 2009), and seed (Saatkamp et al., 2019) spectra have done. Advancing the FES is particularly timely and necessary in the Anthropocene, an epoch characterized by pollinator decline (González-Varo et al., 2013), global temperature changes, and increased occurrence and intensity of drought worldwide (Gallagher & Campbell, 2017; Phillips et al., 2018). Understanding how these changes in pollinators and nonpollinator agents affect the evolution of floral form and function across the flowering plants requires a comparative, mechanistic understanding of how multiple agents of selection act on flowers.

Flowers are multifunctional and subject to multiple agents of selection

Historically, pollinators have been considered the main agents of selection driving the evolution of floral traits (Kölreuter, 1761; Sprengel, 1793; Darwin, 1862; Stebbins, 1950; Stanton et al., 1986). However, mounting evidence over the last three decades has shown that nonpollinator agents of selection also affect the evolution of floral traits (e.g. Ashman & Schoen, 1994; Galen, 1999; Irwin, 2006; Gallagher & Campbell, 2017; Rusman et al., 2019). These nonpollinator agents include abiotic factors, such as climatic conditions and resource availability, and floral enemies, such as nectar robbers, nectar thieves, and florivores. Environmental conditions and resource availability influence floral trait expression, on average, as much as selection by pollinators (Caruso et al., 2019), and enemies such as florivores and nectar robbers hinder pollinator attraction (Moreira et al., 2019). Despite the considerable role of nonpollinator agents of selection, the multiple drivers acting on floral traits are rarely studied in unison (Supporting Information Fig. S1), with most studies of selection in plants or animals manipulating only one selective agent (Caruso et al., 2017).

Because nonpollinator agents of selection can either oppose or reinforce selection by pollinator agents (Strauss & Whittall, 2006), selection by nonpollinator agents cannot be understood without explicitly testing for their effects. Nonpollinator agents of selection can affect floral traits in multiple ways. They can affect floral traits directly, either by acting on traits related to reproductive assurance (e.g. drought reduces flower size; Galen, 1999) or by acting on floral traits that may not themselves be related directly to reproductive assurance but that may affect other floral functions (e.g. florivores may influence the expression of chemical defensive compounds in nectar, Sosenski & Parra-Tabla, 2019; flowers may respond to nectar robbers by producing involutions that incur a higher carbon cost; Guzmán et al., 2017). Nonpollinator agents of selection can

also affect flowers indirectly, by acting on other organs that affect floral traits (e.g. selection on leaf size can affect inflorescence size via Corner's rules; Midgley & Bond, 1989; Lauri, 2019; individuals that have larger leaves typically have fewer axillary buds for inflorescence development; Trejo *et al.*, 2018; Ramos & Schiestl, 2019). The presence of multiple agents of selection, the diversity of ways by which nonpollinator agents can affect floral traits, and the ability of nonpollinator agents to either reinforce or oppose pollinator-mediated selection together likely increase the range of floral trait variation both within and among species (Niklas, 1994; Galen, 1999; Strauss & Whittall, 2006). Using an economics framework that incorporates the costs and multivariate trait trade-offs would better define how multiple selective agents may influence observed optimum trait values and their evolvability, allow for identification of the major axes of variation in flower traits, and expand our understanding of how floral traits are integrated in the entire plant.

The functional 'economics' of flowers

Plant economics spectra are axes of trait covariation that emerge from trade-offs and adaptive covariation in the construction and function of plant organs (Box 1; Agrawal, 2020). Quantifying the economics of a structure is most easily accomplished when the
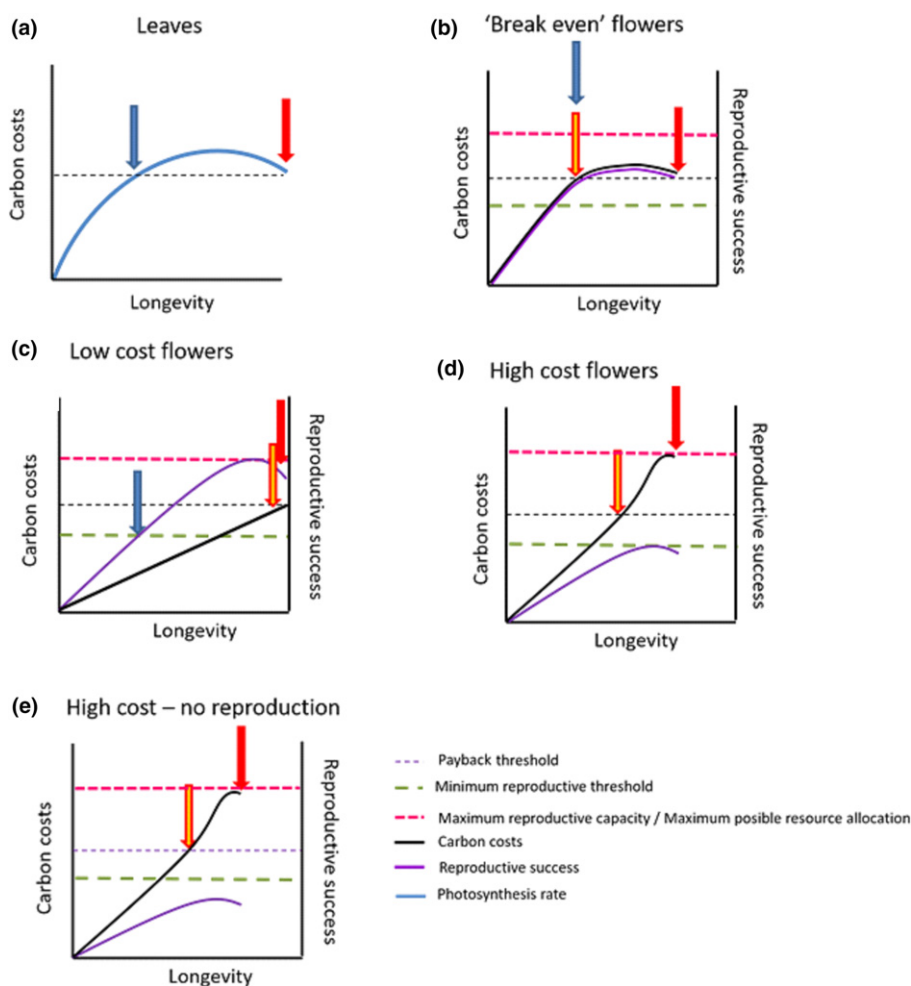

Fig. 1 Economic differences between leaves and flowers. (a) In leaves, a balance between construction costs and carbon fixation determines the minimum viable leaf lifespan (blue arrow) and leaf shedding (red arrow). (b–e) Flowers also have production and maintenance costs (solid black line), but the paybacks are expressed in the form of seed siring and seed production (solid purple line). We propose three benchmarks during flower lifespan: first, the minimum reproductive threshold (dashed green line), at which at least one viable offspring is produced; second, the payback threshold (dashed black line), at which enough offspring are produced to pay back flower production and maintenance costs. After this threshold it is more efficient to produce a new flower than to keep an old flower with high maintenance costs (red arrow); Third, the maximum reproductive capacity (pink dashed line), at which it is assumed that the maximum possible number of seeds per floral unit is produced. This threshold also marks the maximum possible resource allocation an individual can allocate per flower. (b) In 'break even' flowers, maintenance costs and reproductive success increase at the same rate with longevity, so that the production costs (yellow arrow), and reproduction payback threshold (blue arrow) are reached at the same time. (c) In low-cost flowers, maintenance costs increase at a lower rate than reproductive success, so that the reproductive payback threshold is reached before the maintenance payback threshold, allowing floral parts to live long enough to approach the maximum possible reproductive success per flower. (d) In high-cost flowers, maintenance costs increase at a faster rate than reproductive success, and the threshold is reached before the payback reproductive threshold, allowing only the minimum reproductive threshold to be reached. (e) An extreme case of (d), in which the maximum possible resource allocation is reached before the minimum reproductive threshold. In the wild, individuals bearing this kind of flowers should be selected against, but they could be observed under artificial conditions.

resources that are invested in its construction and maintenance and the return on this investment are in comparable units. In leaves, carbon is invested to build a leaf and to maintain its respiratory demand, and the return on this investment occurs as the leaf assimilates carbon throughout its lifetime. More durable leaves that can withstand damage have low instantaneous photosynthetic rates and require a longer lifespan to reap the return on their higher construction costs (Wright *et al.*, 2004). In flowers, the units of investment and return are not directly comparable. Petals (and most petaloid structures) are modified leaves, but the primary function of flowers is seed siring and production, rather than carbon fixation. We suggest, then, that 'economics' refers to the cost–payback relationship that selection should favour, that is, the maintenance costs for a given likelihood of fertilisation and carbon allocation to seeds (Fig. 1, Box 1).

The economics spectrum approach can help in identifying trait trade-offs and in characterising ecological strategies (Agrawal, 2020). At the same time, trait covariation can be used to infer processes of natural selection. In economics spectra of leaves, which have clearly defined units of currency, trade-offs – and their associated vectors of selection – are thought to act similarly across species, such that axes of covariation emerge from interspecific data (Box 1). However, in flowers, the currencies are more difficult to identify because payback thresholds are a balance between costs of flower production and maintenance, likelihood of fertilisation, and carbon allocation to seeds (Fig. 1). Thus, trait covariation in flowers

may encompass a broad functional space, rather than a bivariate spectrum, perhaps with trade-offs occurring among closely related species or among species within the same functional group (e.g. pollination mode) occupying similar regions of this space (Fig. 2; Agrawal, 2020). Such patterns would suggest that how selection acts on flowers may depend on ecological or phylogenetic contexts, which would be difficult to assess without a comparative approach. Synthetically bridging across scales by unifying studies of the effects of floral traits on demographic rates with comparative, interspecific studies (Swenson *et al.*, 2020) would be an important component of developing the FES.

Using an economics spectrum framework would help to identify major functional traits of flowers and the selective pressures shaping floral phenotypic variation. Mating opportunities are temporally limited, and the range of anatomical, chemical, or physiological strategies of flowers may differ from those of leaves, while in other cases traits may covary similarly in leaves and flowers (e.g. Roddy *et al.*, 2019). For example, dry mass per unit area and lifespan are positively related among leaves (Wright *et al.*, 2004) and among corollas in slipper orchids (Zhang *et al.*, 2017). While similar trait scaling relationships may indicate similar selection regimes in both leaves and flowers, flowers may encompass a broader range of traits than leaves, highlighting the diversity of their functions (Roddy *et al.*, 2019). Situations in which flowers deviate from commonly observed positive relationships between floral mass per area (FMA) and
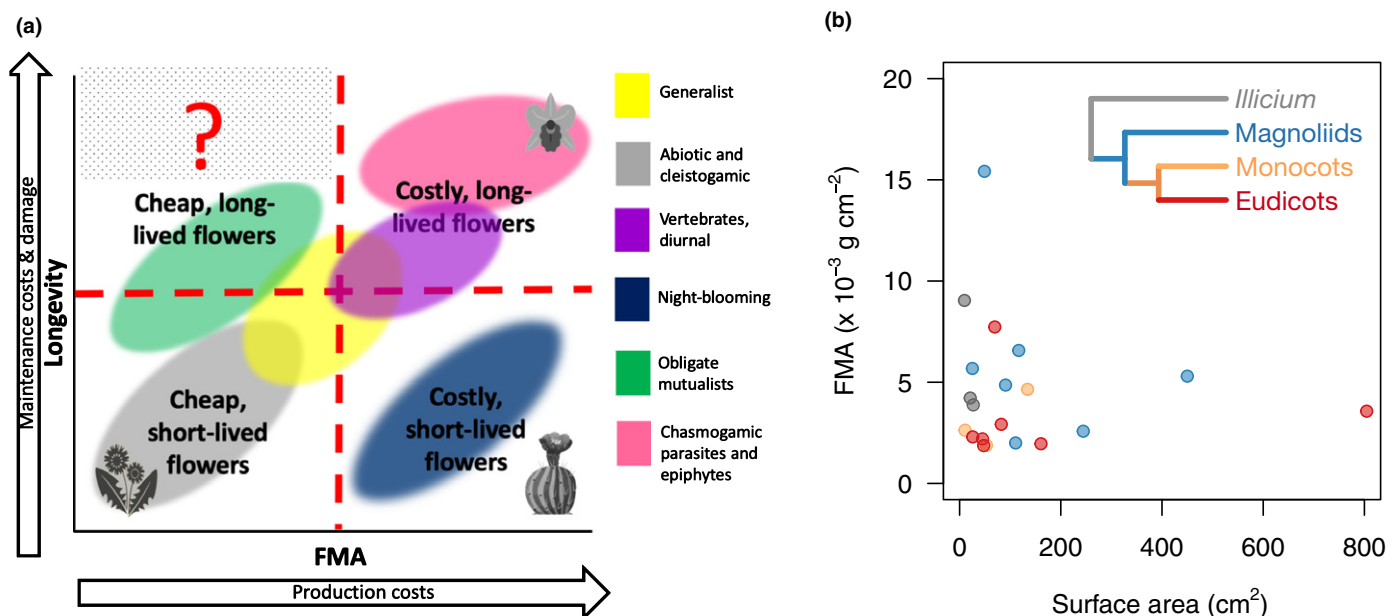

Fig. 2 (a) Hypothetical relationship between flower mass area (FMA) and flower longevity to illustrate the flower economics spectrum. Each quadrant represents possible trait combinations subject to natural selection and is illustrated by iconic examples, such as orchids, cacti, and ruderals, representing extremes in floral allocation and longevity. The FMA–longevity relationship can vary broadly within this space. The oval shadings indicate putative regions of the functional space occupied by (but not restricted to) different floral syndromes that expand the idea beyond pollination to incorporate the three proximate floral functions (attraction, defence, and resistance). The dotted area indicates currently unknown, but hypothesised space either because it is developmentally inaccessible or because it is selected against. Within each floral syndrome a positive relationship between FMA and longevity could be expected as a result of natural selection favouring the most efficient morphotypes for a given set of environmental conditions. The proposed occupied regions and their FMA–longevity relationships should be tested with empirical data. (b) Relationship between flower size and FMA among 20 phylogenetically diverse species. There is no bivariate trade-off at this broad phylogenetic scale. However, there are no species with large flowers and high FMA, suggesting some trait combinations are selected against. Data from Roddy *et al.* (2016).

Box 1 The benefits of thinking in terms of spectra
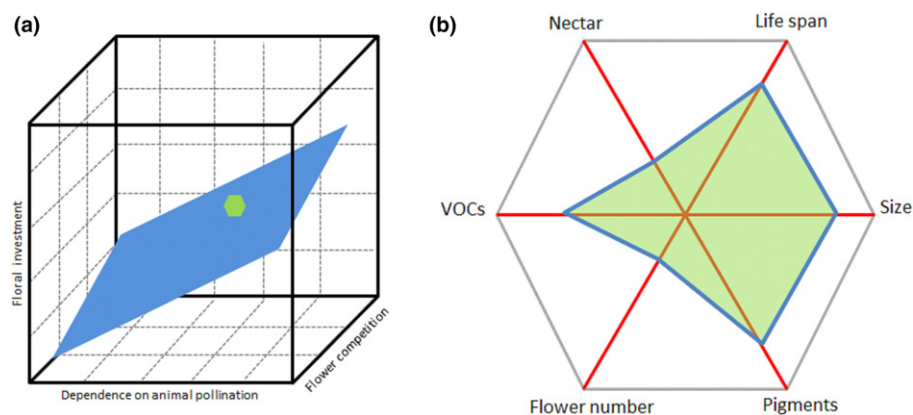
Box Fig. 1 (a) Plant allocation to flower production (carbon (C) allocated to flower production or flower size) may depend on its reliance on animal vectors (seed mass produced by animal pollinations/total seed mass) and on flower competition for pollinators (number of flowering individuals/number of pollinators per unit area/time). The blue shading represents a hypothetical relationship between the three variables, where floral investment is positively correlated with animal pollination dependence and flower competition. The green hexagon represents an example of C allocation as measured in (b). VOCs, volatile organic compounds. (b) Floral costs can be measured in a 'diamond' graph where each vertex represents a functional trait. The shape and the size of the diamond indicate how individuals allocate resources into flower production.

Trait spectra are axes of covariation along which most or at least many plants fall and are useful because they help identify pervasive trade-offs and widespread vectors of selection that shape plant functional diversity. Thinking about flowers in these terms highlights crucial research directions.

One is the likely greater breadth of floral functional diversity as compared to leaves (Roddy *et al.*, 2019). The leaf economics spectrum reveals strong patterns of covariation, as in the marked trade-off between leaf mass per unit area (LMA) and leaf lifespan. The space below this line could be occupied – a plant *could* produce high LMA leaves and shed them immediately. This trait combination, while surely possible, would not recuperate the carbon investment in leaves and would therefore not be favoured relative to other individuals in the population that retain their leaves for longer. In flowers, however, high construction cost and short lifespan seem likely to exist (e.g. *Selenicereus* or *Stapelia* flowers) because selection likely acts to minimise costs per probability of successful reproduction rather than costs per rate of carbon return. Petal mass per unit area and petal lifespan may likely fill a much wider space than their leaf counterparts, but very few data are available to explore these relationships across the angiosperms.

Another crucial research issue that the floral economics spectrum (FES) highlights is that while carbon allocation per unit of carbon fixed provides a common currency for comparing leaves across species (Kikuzawa & Lechowicz, 2006; Selaya & Anten, 2010), it is not clear how to compare carbon investment and return on investment for flowers. Plants invest seemingly large amounts of resources in floral construction, pigments, volatiles, and nutritional rewards. Allocation to these floral attractiveness-related traits depends on how much of the total seed siring and production is the result of animal pollination and access to pollinators (Box Fig. 1a). If floral visitors are scarce, there will be stronger selection towards individuals able to attract more pollinators than if pollinators are not limiting. Pollinator competition can lead to flower specialisation, in which selection favours variants with higher visitation and species-specific cross-fertilisation. However, if pollinators are too scarce, or there are insufficient mating partners for a plant to reach the minimum reproductive threshold (Fig. 1), natural selection would favour individuals that are able to self-fertilise, use abiotic pollen vectors, or reproduce asexually (Maciel *et al.*, 2020). This would lower animal pollination dependence and its associated selective pressure for floral attractiveness. How floral carbon investment is related to reproductive output across species – whether it describes a positive relationship or is a diffuse cloud or a multidimensional space, for example – is unknown, again illustrating the crucial research questions that the FES highlights.

One approach would be to divide floral investment among several components (e.g. Supporting Information Table S1), each of which can be individually and simultaneously measured (Box Fig. 1b). While the shape of the circumscribed trait space (blue line) can be used as a proxy for how individuals partition their flower budget, the area of this trait space (green area) can be used as a measure of total flower costs. This metric can be plotted against dependence on animal pollination and competition for pollinators to better define the shape and dimensions of the FES.

Another promising direction of thinking in spectra is reformulating the idea of floral syndromes, which go beyond pollination syndromes. Floral syndromes can be defined as a set of coordinated traits that incorporate interactions with pollinators and also the adaptive value of deterring enemies and coping with environmental stress. Exploring the idea of floral syndromes requires a multidimensional assessment of floral traits and functions.

longevity highlight the wide diversity of flower functional strategies (Box 1; Teixido *et al.*, 2016, 2019). Such comparative analyses can be used to identify the strength of selective agents and their dependence on ecological or phylogenetic contexts, in contrast to the possibility that many traits covary due to developmental constraints (Olson & Pittermann, 2019).

Thus, using knowledge about leaves as a baseline can help to identify what may be general principles in building aerial plant structures versus the axes along which divergent functions have driven divergent floral forms (Roddy *et al.*, 2013, 2016). Moreover, that many traits are and possibly could be involved in pollination necessitates moving beyond studies of bivariate trait relationships to include multivariate approaches (Chartier *et al.*, 2014) that showcase the many potential combinations of different traits and trait values that underlie phenotypic evolution (Whibley *et al.*, 2006; Chartier *et al.*, 2017). Furthermore, understanding multivariate trait evolution inevitably requires collection of standardised floral traits.

Trait covariation and the primary dimensions of floral traits

Flower function can be thought of as having three primary selective pressures: reproductive assurance, enemy deterrence, and stress resistance. Flowers are composed of multiple organs, some of which are absent in some lineages. All of these functions and the structures that perform them must be tightly coordinated to enable seed siring and production (Figs 1, 2; Berg, 1960; Baranzelli *et al.*, 2014; Diggle, 2014). Among these organs, one of the most important is the corolla, which attracts pollinators and protects other organs, and which, because of its size, placement, and function, can be physiologically costly (Galen, 1999; Field *et al.*, 2009; Roddy & Dawson, 2012; Teixido & Valladares, 2014; Roddy *et al.*, 2018). The physiological costs of constructing and maintaining flowers can affect key reproductive traits such as floral longevity (Ashman & Schoen, 1994; Zhang *et al.*, 2017), and flowers may have been under selection to reduce these physiological costs (Fig. 2; Roddy *et al.*, 2016, 2019; Roddy, 2019). For example, flowers can reduce physiological construction and maintenance costs by building 'cheaper' structures with low FMA, potentially at the cost of shorter longevity and smaller size (Fig. 2a). The limited empirical data available suggest that there is a triangular relationship between flower size and FMA, such that small flowers can be either cheap or expensive per unit area, but large flowers must be cheap (Fig. 2b; Roddy *et al.*, 2016). Flower longevity, which is intimately tied to the probability of reproduction, likely covaries orthogonally to the FMA–flower size relationship and may help to explain its triangularity. The relative effects of nonpollinator agents and pollinators on floral traits related to the three primary functions may vary across environmental gradients (Lambrecht & Dawson, 2007; Lambrecht, 2013), in different plant–pollinator communities (Campbell & Powers, 2015), or among different lineages (Roddy *et al.*, 2016).

Comparative studies of flowers are necessary to construct the FES but are hindered by the lack of common, standardised trait measurements (but see Paterno *et al.*, 2020). Even seemingly simple quantitative traits such as flower size are measured inconsistently among different taxonomic groups and among different disciplines (Roddy, 2019), limiting the utility of individual studies and preventing their incorporation into global databases (e.g. Kattge *et al.*, 2020) and comparative analyses (e.g. Sauquet *et al.*, 2017). Therefore, we propose that as a first step towards constructing the FES, standardised measurements of flower size, longevity, and biomass allocation should be taken (Box 2). Such broad sampling would identify patterns of covariation between these traits that are observed across all or most species, as well as those that are specific to certain functional or phylogenetic contexts (Fig. 2). These traits can be measured universally on corollas and are related to the three primary functions of flowers, enabling detection of pervasive patterns (Box 1; e.g. Koski & Ashman, 2016; Delmas *et al.*, 2020; Paterno *et al.*, 2020) that may be related to other macroevolutionary patterns of floral evolution (e.g. Stebbins, 1951; Hodges & Arnold, 1995; O'Meara *et al.*, 2016). Focusing initially on the showy perianth structures would provide a viable baseline for further expansion of the FES to include additional floral traits and the other organs that comprise flowers and their associated functions. In addition to these primary traits, we also suggest a secondary set of allocational, phenological, physiological, chemical, morphological, and anatomical traits that may later advance multivariate dimensions of the FES (Table S1; Box 2).

Extensions of the FES

Employing an economics spectrum approach promises to enrich our understanding of the processes driving and responding to floral trait diversity spanning spatial scales from the organismal to the community and over evolutionary timescales. Constructing the first iteration of the FES, as we have suggested here, would allow testing of whether trait covariation patterns vary among flower functional groups (e.g. pollination syndromes) and identifying the biophysical limits of and constraints on flower functional space. Data collected as part of this initial iteration of the FES could be extended to advance numerous pressing questions. First, when combined with data for other plant organs, these floral data could be used further to test theories about modularity and phenotypic integration (Berg, 1960) due to either common developmental programs in disparate plant organs or to selection acting on certain trait combinations (Midgley & Bond, 1989; Pélabon *et al.*, 2013; Roddy *et al.*, 2013, 2019). Measuring common traits would guide identification of the functional basis for the disparities between organs (Olson & Pittermann, 2019; Roddy *et al.*, 2019) while enabling comparisons with the economics spectra for other plant structures in order to generate whole plant functional axes (Díaz *et al.*, 2016) related to life history (Stearns, 1989). Second, flowers and their specialised interactions with animal pollinators are commonly assumed to promote diversification (van der Kooi & Ollerton, 2020), yet relatively few studies have assessed angiosperm-wide floral trait diversity (O'Meara *et al.*, 2016; Sauquet *et al.*, 2017). The data required to build this first iteration of the FES would enable more rigorous examination of ideas about the evolution of floral form in response to multiple agents of selection. Third, building the FES would better integrate floral traits into studies of community assembly (Sargent & Ackerly, 2008; Bruelheide *et al.*, 2018; E-Vojtkó *et al.*, 2020). The global decline of pollinators suggests that competition for pollinators may cause floral traits to become even more important in maintaining the resilience of ecological communities (Thomann *et al.*, 2013).

Without a conceptual framework that synthesizes floral trait relationships across disciplines, our understanding of the interplay between the multiple floral functions and constraints will remain limited. Now is the time to unite traditionally disparate disciplines, to develop standardised floral trait measurements, and to identify their functional significance. We have proposed that characterising the floral economics spectrum would better identify both how traits influence floral functions and how selection on these functions in different ecological or phylogenetic contexts affects floral trait expression. While we have focused primarily on the corolla, other organs (e.g. bracts, sepals, carpels, and stamens) may each have their own functional dimensions. For some of these organs, the functional dimensions may be similar to those we have proposed for corollas (e.g. sepals and bracts), but for others there may be

---

Box 2 Standardising measurements for the floral economics spectrum (FES)

A global database of standardised floral traits is needed to empirically test and validate the FES. Proposals for standardisation of floral traits have focused mostly on pollination-related traits (Dafni *et al.*, 2005), which are insufficient to develop the first iteration of the FES. We provide here detailed guidelines to sample three key functional traits related to the major axes of the FES (Fig. 2). As a general principle, we recommend focusing measurements on the showy perianth structures, most commonly the corolla. However, it is unlikely that any standardised protocol will be able to capture the full variation of the angiosperms.

Flower size

Definition and significance Flower size encompasses many different metrics of measuring how large a flower is. The metrics of size commonly used depend on the ease of measurement and the inferred functional significance of the metric (e.g. tubular flowers are commonly measured in terms of length or diameter, which are thought to influence pollinator specificity). Some metrics of flower size are strongly correlated with the single-sided projected surface area (Roddy, 2019), which we suggest to be the most generally relevant metric.

Methodology Individual petals can be dissected from the rest of the flower and their two-dimensional projected surface area measured with a flatbed scanner or digital camera by pressing them gently under a glass plate with an adjacent size calibration. Curved, fused, or tubular structures can be dissected into approximately flat pieces and their areas measured similarly. Summing across dissected pieces or petals yields the total flower area. Preferably fresh, fully hydrated, and undamaged flowers should be used.

Unit of measurement cm^2.

Floral longevity

Definition and significance Floral longevity is the length of time that a flower remains open in the field and functionally active. Floral longevity ranges from a few hours to several weeks (Primack, 1985; Ashman & Schoen, 1994). Although longer longevity increases the probability of reproductive success by favouring pollen removal and pollen deposition, it also entails costs, especially related to water use for nectar production and transpirational cooling and carbon for respiration (Ashman & Schoen, 1997; Castro *et al.*, 2008; Teixido *et al.*, 2019). Consequently, the evolution of floral longevity is thought to be shaped by natural selection to maximise pollen transfer while minimising floral maintenance costs (Ashman & Schoen, 1994, 1996).

Methodology Measurements should start immediately upon flower opening when the perianth appears fresh and end upon either corolla abscission or corolla or stamen wilting or discoloration (Primack, 1985). Floral longevity can be estimated observationally by tagging individual flower buds.

Experimental manipulation of floral longevity can be conducted by pollination treatments (e.g. Giblin, 2005; Castro *et al.*, 2008; Arroyo *et al.*, 2013; Teixido *et al.*, 2019). Pathogen- and herbivore-free, open and functionally active flowers from each individual can be assigned to one of three treatments – hand-pollinated with xenogamous pollen, pollination-excluded, and unmanipulated (i.e. naturally pollinated) flowers – within the same individual to control for individual variation. Outcrossed pollen can be manually deposited on the stigma using cotton swabs, small brushes, toothpicks, or by direct contact of anthers from donor flowers (reviewed in Willmer, 2011). Potential pollinators can be

excluded using bags, cages, nets or insect repellents, although capping stigmas with straws or modelling clay is desirable because it is minimally invasive and avoids altering environmental conditions that may affect floral longevity (Dafni *et al.*, 2005; Teixido & Valladares, 2015).

Unit of measurement Days, or alternatively hours or weeks for very brief or very long flowering species, respectively, with sufficient precision to allow conversion between units.

Flower mass per area

Definition and significance Flower mass per area (FMA) is the dry mass of a fresh flower divided by its single-sided projected surface area. FMA is positively correlated with corolla lifespan in slipper orchids (Zhang *et al.*, 2017) and with water allocation and use (Roddy *et al.*, 2016; Teixido *et al.*, 2019), but measurements remain limited.

Methodology Pathogen- and herbivore-free, open and functionally active flowers should be used. Surface area should be determined as explained in the Flower size section, earlier. After area measurements, put each petal or corolla in the oven, ideally at 70°C for at least 72 h, or at 80°C for 48 h; and subsequently weigh the dry mass (Pérez-Harguindeguy *et al.*, 2013).

Unit of measurement $g\ m^{-2}$.

---

different functional dimensions not addressed here. For each of these organs, the relative importance of different functions may vary throughout floral development. Incorporating other organs and a developmental framework would further improve our understanding of the interplay between floral morphology and natural selection and open new avenues of research to continue refining and testing the FES.

Acknowledgements

Author contributions

ABR, CM-P, ALT, TGC, MEO, RSO and FAOS planned and designed the research. All authors wrote, edited, and revised the manuscript and approved the final version.

ORCID

Tatiana G. Cornelissen https://orcid.org/0000-0002-2721-7010
Cecilia Martínez-Perez https://orcid.org/0000-0002-8729-1781

Rafael S. Oliveira (ID) https://orcid.org/0000-0002-6392-2526
Mark E. Olson (ID) https://orcid.org/0000-0003-3715-4567
Adam B. Roddy (ID) https://orcid.org/0000-0002-4423-8729
Fernando A. O. Silveira (ID) https://orcid.org/0000-0001-9700-7521
Alberto L. Teixido (ID) https://orcid.org/0000-0001-8009-1237

Adam B. Roddy[1] (ID) **, Cecilia Martínez-Perez[2]** (ID) **, Alberto L. Teixido[3]** (ID) **, Tatiana G. Cornelissen[4]** (ID) **, Mark E. Olson[2]** (ID) **, Rafael S. Oliveira[5]** (ID) **and Fernando A. O. Silveira[4]*** (ID)

[1]School of the Environment, Yale University, 370 Prospect St, New Haven, CT 06511, USA;
[2]Instituto de Biología, Universidad Nacional Autónoma de México, Tercer Circuito s/n de Ciudad Universitaria, Ciudad de México 04510, Mexico;
[3]Departamento de Botânica e Ecologia, Universidade Federal do Mato Grosso, Cuiabá 78060-634, Brazil;
[4]Departamento de Genética, Ecologia e Evolução, Universidade Federal de Minas Gerais, Belo Horizonte 31270-901, Brazil;
[5]Departamento de Biologia Vegetal, Universidade Estadual de Campinas, Campinas 13083-862, Brazil
(*Author for correspondence: tel +55 31 34092609; email faosilveira@icb.ufmg.br)

References

Agrawal AA. 2020. A scale-dependent framework for trade-offs, syndromes, and specialization in organismal biology. *Ecology* **101**: e02924.

Arroyo MTK, Dudley LS, Jespersen G, Pacheco DA, Cavieres LA. 2013. Temperature-driven flower longevity in a high-alpine species of *Oxalis* influences reproductive assurance. *New Phytologist* **200**: 1260–1268.

Ashman TL, Schoen DJ. 1994. How long should flowers live? *Nature* **371**: 788–791.

Ashman TL, Schoen DJ. 1996. Floral longevity: fitness consequences and resource costs. In: Lloyd DG, Barrett SCH, eds. *Floral biology*. New York, NY, USA: Chapman & Hall, 112–139.

Ashman TL, Schoen DJ. 1997. The cost of floral longevity in *Clarkia tembloriensis*: an experimental investigation. *Evolutionary Ecology* **11**: 289–300.

Baranzelli MC, Sérsic AN, Cocucci AA. 2014. The search for Pleiades in trait constellations: functional integration and phenotypic selection in the complex flowers of *Morrenia brachystephana* (Apocynaceae). *Journal of Evolutionary Biology* **27**: 724–736.

Berg RL. 1960. The ecological significance of correlation Pleiades. *Evolution* **14**: 171–180.

Bruelheide H, Dengler J, Purschke O, Lenior J, Jiménez-Alfaro B, Hennekens SM, Botta-Dukát Z, Chytry Milan, Field R, Jansen F et al. 2018. Global trait–environment relationships of plant communities. *Nature Ecology & Evolution* **2**: 1906–1917.

Campbell DR, Powers JM. 2015. Natural selection on floral morphology can be influenced by climate. *Proceedings of the Royal Society B: Biological Sciences* **282**: 20150178.

Caruso CM, Eisen KE, Martin RA, Sletvold N. 2019. A meta-analysis of the agents of selection on floral traits. *Evolution* **73**: 4–14.

Caruso CM, Martin RA, Sletvold N, Morrissey MB, Wade MJ, Augustine KE, Carlson SM, MacColl ADC, Siepielski AM, Kingsolver JG. 2017. What are the environmental determinants of phenotypic selection? A meta-analysis of experimental studies. *American Naturalist* **190**: 363–376.

Castro S, Silveira P, Navarro L. 2008. Effect of pollination on floral longevity and costs of delaying fertilization in the out-crossing *Polygala vayredae* Costa (Polygalaceae). *Annals of Botany* **102**: 1043–1048.

Chartier M, Jabbour F, Gerber S, Mitteroecker P, Sauquet H, von Balthazar M, Staedler Y, Crane PR, Schönenberger J. 2014. The floral morphospace – a modern comparative approach to study angiosperm evolution. *New Phytologist* **204**: 841–853.

Chartier M, Löfstrand S, von Balthazar M, Gerber S, Jabbour F, Sauquet H, Schönenberger J. 2017. How (much) do flowers vary? Unbalanced disparity among flower functional modules and a mosaic pattern of morphospace occupation in the order Ericales. *Proceedings of the Royal Society B: Biological Sciences* **284**: 20170066.

Chave J, Coomes D, Jansen S, Lewis SL, Swenson NG, Zanne AE. 2009. Towards a worldwide wood economics spectrum. *Ecology Letters* **12**: 351–366.

Dafni A, Kevan PG, Husband B. 2005. *Practical pollination biology*. Cambridge, Canada: Enviroquest.

Darwin C. 1862. *On the various contrivances by which British and foreign orchids are fertilized by insects*. London, UK: John Murray.

Delmas CEL, Kooyman RM, Rossetto M. 2020. Evolutionary constraints and adaptation shape the size and colour of rain forest fruits and flowers at continental scale. *Global Ecology and Biogeography* **29**: 830–841.

Díaz S, Kattge J, Cornelissen JHC, Wright IJ, Lavorel S, Dray S, Reu B, Kleyer M, Wirth C, Prentice IC et al. 2016. The global spectrum of plant form and function. *Nature* **529**: 167–171.

Diggle PK. 2014. Modularity and intra-floral integration in metameric organisms: plants are more than the sum of their parts. *Proceedings of the Royal Society B: Biological Sciences* **369**: 20130253.

Donovan LA, Maherali H, Caruso CM, Huber H, de Kroon H. 2011. The evolution of the worldwide leaf economics spectrum. *Trends in Ecology & Evolution* **26**: 88–95.

E-Vojtkó A, de Bello F, Durka W, Kühn I, Götzenberger L. 2020. The neglected importance of floral traits in trait-based community assembly. *Journal of Vegetation Science* **31**: 529–239.

Feild TS, Chatelet DS, Brodribb TJ. 2009. Giant flowers of southern magnolia are hydrated by the xylem. *Plant Physiology* **150**: 1587–1597.

Galen C. 1999. Why do flowers vary? The functional ecology of variation in flower size and form within natural plant populations. *BioScience* **49**: 631–640.

Gallagher MK, Campbell DR. 2017. Shifts in water availability mediate plant–pollinator interactions. *New Phytologist* **215**: 792–802.

Giblin DE. 2005. Variation in floral longevity between populations of *Campanula rotundifolia* (Campanulaceae) in response to fitness accrual rate manipulation. *American Journal of Botany* **92**: 1714–1722.

González-Varo JP, Biesmeijer JC, Bommarco R, Potts SG, Schweiger O, Smith HG, Steffan-Dewenter I, Szentgyörgi H, Woyciechowki M, Vilà M. 2013. Combined effects of global change pressures on animal-mediated pollination. *Trends in Ecology and Evolution* **28**: 524–530.

Guzmán B, Gómez JM, Vargas P. 2017. Is floral morphology a good predictor of floral visitors to Antirrhineae (snapdragons and relatives)? *Plant Biology* **19**: 515–524.

Hodges SA, Arnold ML. 1995. Spurring plant diversification: are floral nectar spurs a key innovation? *Proceedings of the Royal Society B* **262**: 343–348.

Irwin RE. 2006. The consequences of direct versus indirect species interactions to selection on traits: pollination and nectar robbing in *Ipomopsis aggregate*. *American Naturalist* **167**: 315–328.

Kattge J, Bönisch G, Diaz S, Lavorel S, Prentice IC, Leadley P et al. 2020. TRY plant trait database – enhanced coverage and open access. *Global Change Biology* **26**: 119–188.

Kikuzawa K, Lechowicz MJ. 2006. Toward synthesis of relationships among leaf longevity, instantaneous photosynthetic rate, lifetime leaf carbon gain, and the gross primary production of forests. *American Naturalist* **168**: 373–383.

Kölreuter JG. 1761. *Vorläufige Nachricht von einigen das Geschlecht der Pflanzen betreffenden Versuchen und Beobachtungen*. Leipzig, Germany: Gleditsch.

Koski MH, Ashman T-L. 2016. Macroevolutionary patterns of ultraviolet floral pigmentation explained by geography and associated bioclimatic factors. *New Phytologist* **211**: 708–718.

Lambrecht SC. 2013. Flower water costs and size variation in the highly selfing *Leptosiphon bicolor* (Polemoniaceae). *International Journal of Plant Sciences* **174**: 74–84.

Lambrecht SC, Dawson TE. 2007. Correlated variation of floral and leaf traits along a moisture availability gradient. *Oecologia* **151**: 574–583.

Lauri PE. 2019. Corner's rule as a framework for plant morphology, architecture and functioning – issues and steps forward. *New Phytologist* 221: 1679–1684.

Maciel AA, Cardoso JCF, Oliveira PE. 2020. On the low reproductive success of two *Cyrtopodium* species (Orchidaceae: Cyrtopodiinae): the relative roles of biotic and abiotic pollination. *Plant Species Biology* 35: 49–58.

Midgley JJ, Bond WJ. 1989. Leaf size and inflorescence size may be allometrically related traits. *Oecologia* 78: 427–429.

Moreira X, Castagneyrol B, Abdala-Roberts L, Traveset A. 2019. A meta-analysis of herbivore effects on plant attractiveness to pollinators. *Ecology* 100: e02707.

Niklas KJ. 1994. *Plant allometry: the scaling of form and process.* Chicago, IL, USA: University of Chicago Press.

O'Meara BC, Smith SD, Armbruster SC, Harder LD, Hardy CR, Hileman LC, Hufford L, Litt A, Magallón S, Smith SA *et al.* 2016. Non-equilibrium dynamics and floral trait interactions shape extant angiosperm diversity. *Proceedings of the Royal Society B: Biological Sciences* 283: 20152304.

Olson ME, Pittermann J. 2019. Cheap and attractive: water relations and floral adaptation. *New Phytologist* 223: 8–10.

Paterno GB, Silveira CL, Kollmann J, Westoby M, Fonseca CR. 2020. The maleness of larger angiosperm flowers. *Proceedings of the National Academy of Sciences, USA* 117: 10921–10926.

Pélabon C, Osler NC, Diekmann M, Graae BJ. 2013. Decoupled phenotypic variation between floral and vegetative traits: distinguishing between developmental and environmental correlations. *Annals of Botany* 111: 935–944.

Phillips BB, Shaw RF, Holland MJ, Fry EL, Bardgett RD, Bullock JM, Osborne JL. 2018. Drought reduces floral resources for pollinators. *Global Change Biology* 24: 3226–3235.

Primack RB. 1985. Longevity of individual flowers. *Annual Review of Ecology and Systematics* 16: 15–37.

Ramos SE, Schiestl FP. 2019. Rapid plant evolution driven by the interaction of pollination and herbivory. *Science* 364: 193–196.

Roddy AB. 2019. Energy balance implications of floral traits involved in pollinator attraction and water balance. *International Journal of Plant Sciences* 180: 944–953.

Roddy AB, Brodersen CR, Dawson TE. 2016. Hydraulic conductance and the maintenance of water balance in flowers. *Plant, Cell & Environment* 39: 2123–2132.

Roddy AB, Dawson TE. 2012. Determining the water dynamics of flowering using miniature sap flow sensors. *Acta Horticulturae* 951: 47–54.

Roddy AB, Guilliams CM, Lilittham T, Farmer J, Wormser V, Pham T, Fine PVA, Feild TS, Dawson TE. 2013. Uncorrelated evolution of leaf and petal venation patterns across the angiosperm phylogeny. *Journal of Experimental Botany* 64: 4081–4088.

Roddy AB, Jiang GF, Cao K, Simonin KA, Brodersen CR. 2019. Hydraulic traits are more diverse in flowers than in leaves. *New Phytologist* 223: 193–203.

Roddy AB, Simonin KA, McCulloh KA, Brodersen CR, Dawson TE. 2018. Water relations of *Calycanthus* flowers: hydraulic conductance, capacitance, and embolism resistance. *Plant, Cell & Environment* 41: 2250–2262.

Rusman Q, Lucas-Barbosa D, Poelman EH, Dicke M. 2019. Ecology of plastic flowers. *Trends in Ecology and Evolution* 24: 725–740.

Saatkamp A, Cochrane A, Commander L, Guja LK, Jimenez-Alfaro B, Larson J, Nicotra A, Poschlod P, Silveira FAO, Cross AT *et al.* 2019. A research agenda for seed-trait functional ecology. *New Phytologist* 221: 1764–1775.

Sargent RD, Ackerly DD. 2008. Plant–pollinator interactions and the assembly of plant communities. *Trends in Ecology and Evolution* 23: 123–130.

Sauquet H, von Balthazar M, Magallón S, Doyle JA, Endress PK, Bailes EJ, de Morais EB *et al.* 2017. The ancestral flower of angiosperms and its early diversification. *Nature Communications* 8: 16047.

Selaya NG, Anten NPR. 2010. Leaves of pioneer and later-successional trees have similar lifetime carbon gain in tropical secondary forest. *Ecology* 91: 1102–1113.

Sosenski P, Parra-Tabla V. 2019. *Secondary metabolites: attracting pollinators.* eLS. Chichester, UK: John Wiley & Sons. doi: 10.1002/9780470015902.a0000909.pub2.

Sprengel CK. 1793. *Das entdeckte Geheimnis der Natur im Bau und in der Befruchtung der Blumen.* Berlin, Germany: Friedrich Vieweg.

Stanton ML, Snow AA, Handel SN. 1986. Floral evolution: attractiveness to pollinators increases male fitness. *Science* 232: 1625–1627.

Stearns SC. 1989. Trade-offs and life-history evolution. *Functional Ecology* 3: 259–268.

Stebbins GL. 1950. *Variation and evolution in plants.* New York, NY, USA: Columbia University Press.

Stebbins GL. 1951. Natural selection and the differentiation of angiosperm families. *Evolution* 5: 299–324.

Strauss SY, Whittall JB. 2006. Non-pollinator agents of selection on floral traits. In: Harder LD, Barrett SCH, eds. *Ecology and evolution of flowers.* Oxford, UK: Oxford University Press, 120–138.

Swenson NG, Worthy SJ, Eubanks D, Iida Y, Monks L, Petprakob K, Rubio VE, Staiger K Zambrano J. 2020. A reframing of trait–demographic rate analyses for ecology and evolutionary biology. *International Journal of Plant Sciences* 181: 33–43.

Teixido AL, Barrio M, Valladares F. 2016. Size matters: understanding the conflict faced by large flowers in Mediterranean environments. *Botanical Review* 82: 204–228.

Teixido AL, Leite-Santos VB, Paiva EAS, Silveira FAO. 2019. Water-use strategies in flower from a neotropical savanna under contrasting environmental conditions during flowering. *Plant Physiology and Biochemistry* 144: 283–291.

Teixido AL, Valladares F. 2014. Disproportionate carbon and water maintenance costs of large corollas in hot Mediterranean ecosystems. *Perspectives in Plant Ecology, Evolution and Systematics* 16: 83–92.

Teixido AL, Valladares F. 2015. Temperature-limited floral longevity in the large-flowered mediterranean shrub *Cistus ladanifer* (Cistaceae). *International Journal of Plant Sciences* 176: 131–140.

Thomann M, Imbert E, Devaux C, Cheptou PO. 2013. Flowering plants under global pollinator decline. *Trends in Plant Science* 18: 353–359.

Trejo L, Rosell JA, Olson ME. 2018. Nearly 200 years of sustained selection have not overcome the leaf area-stem size relationship in the poinsettia. *Evolutionary Applications* 11: 1401–1411.

Whibley AC, Langlade NB, Andalo C, Hanna AI, Bangham A, Thébaud C, Coen E. 2006. Evolutionary paths underlying flower color variation in *Antirrhinum. Science* 313: 963–966.

Willmer P. 2011. *Pollination and floral ecology.* Princeton, NJ, USA: Princeton University Press.

Wright IJ, Reich PB, Westoby M, Ackerly DD, Baruch Z, Bongers F *et al.* 2004. The worldwide leaf economics spectrum. *Nature* 428: 821–827.

Zhang FP, Yang YJ, Yang QY, Zhang W, Brodribb TJ, Hao GY, Hu H, Zhang SB. 2017. Floral mass per area and water maintenance traits are correlated with floral longevity in *Paphiopedilum* (Orchidaceae). *Frontiers in Plant Sciences* 8: 501.

Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Fig. S1 Data on the phylogenetic and geographic distribution of studies addressing agents of selection on floral traits.

Table S1 Nonexhaustive list of key flower traits to be sampled across biomes and lineages to improve our understanding of the flower economics spectrum.

Please note: Wiley Blackwell are not responsible for the content or functionality of any Supporting Information supplied by the authors. Any queries (other than missing material) should be directed to the *New Phytologist* Central Office.