

## Viewpoint

# The dynamic mosaic phenotypes of flowering plants

### Summary

Ecological interaction and adaptation both depend on phenotypic characteristics. In contrast with the common conception of the 'adult' phenotype, plant bodies develop continuously during their lives. Furthermore, the different units (metamers) that comprise plant bodies are not identical copies, but vary extensively within individuals. These characteristics foster recognition of plant phenotypes as dynamic mosaics. We elaborate this conception based largely on a wide-ranging review of developmental, ecological and evolutionary studies of plant reproduction, and identify its utility in the analysis of plant form, function and diversification. An expanded phenotypic conception is warranted because dynamic mosaic features affect plant performance and evolve. Evidence demonstrates that dynamic mosaic phenotypes enable functional ontogeny, division of labour, resource and mating efficiency. In addition, dynamic mosaic features differ between individuals and experience phenotypic selection. Investigation of the characteristics and roles of dynamic and mosaic features of plant phenotypes benefits from considering within-individual variation as a function-valued trait that can be analysed with functional data methods. Phenotypic dynamics and within-individual variation arise despite an individual's genetic uniformity, and develop largely by heterogeneous gene expression and associated hormonal control. These characteristics can be heritable, so that dynamic mosaic phenotypes can evolve and diversify by natural selection.

### Introduction

Ecology and adaptive evolution poise on the phenotypes of individual organisms. An organism's biochemical, physiological, morphological and behavioural characteristics set its capacity to function in a specific environment. Interaction of an individual's phenotype with the opportunities and limitations presented by the environment govern its realised growth, survival and reproduction. In turn, populations grow or decline, affecting community composition, ecosystem energy flows and nutrient cycles. If phenotypic dissimilarity among individuals causes differential survival and reproduction and is genetically determined, alleles associated with more successful phenotypes will be more common in the next generation (Endler, 1986; Barrett *et al.*, 2019). Such

evolution alters the population's genetic structure and enhances its environmental interaction, further affecting population, community and ecosystem organisation and dynamics (Bolnick *et al.*, 2011). Therefore, the phenotype is the nexus of biological diversity, being both an organism's interface with its environment and a population's vehicle of adaptation.

Despite its ecological and evolutionary significance, perspectives on the phenotype are often limited. For example, thousands of studies of phenotypic selection (Harder & Johnson, 2009; Kingsolver *et al.*, 2012) have assessed phenotypic selection using single measurements of traits of adult individuals. This approach implies that an individual's phenotype is static and uniform. Stasis may be relevant for qualitative traits, but this is rarely true of continuous traits, if they develop during an individual's life (Fusco, 2001; Donohue, 2014). Phenotypic uniformity at a given developmental stage may be pertinent for organs, behaviours, and so on, that occur once per individual, but not necessarily for those with multiple realisations. Therefore, static uniformity will often misrepresent an individual's phenotype, its function and evolutionary relevance (Diggle, 2003, 2014; Kingsolver *et al.*, 2015; Herrera, 2017).

Static uniformity is particularly inappropriate as a phenotypic conception for metameric organisms such as plants and Cnidarians. The bodies of such organisms (hereafter plants) are integrated collections of repeated units (metamers: Barlow, 1989). Plants grow primarily by adding metamers, rather than enlargement of each organ type, as in unitary animals. Such growth is enabled by retention of pluripotent cells in meristems, which allows postembryonic morphogenesis (Greb & Lohmann, 2016). Consequently, organ initiation (including sex organs) and growth (including regeneration and possibly clonal propagation) occur throughout life, even after reproduction begins (Gaillochet & Lohmann, 2015). These architectural and ontogenetic plant characteristics generate dynamic phenotypes (Sattler, 1990; Minelli, 2018), involving ongoing birth, development and (programmed) death of metamers (White, 1979). Furthermore, a plant is a phenotypic mosaic if its organ copies differ developmentally, structurally and physiologically (see Barrett & Harder, 1992; Diggle, 2003). For clonal plants, this mosaic includes the physical individuals (ramets) that comprise the genetic individual (genet) (Charpentier & Stuefer, 1999; Hämmerli & Reusch, 2003). Consequently, a plant's dynamic mosaic phenotype includes the entire spatial and temporal within-genet distribution of its components (also see Diggle, 2003; Herrera, 2009; Kulbaba *et al.*, 2017). Furthermore, a genet's performance depends on the integrated outcomes of all its metamers during all their developmental stages (Harder *et al.*, 2004; Vallejo-Marín *et al.*, 2010; Donohue, 2014).

Here, we elaborate the concept of the dynamic mosaic phenotype of plants and consider its developmental, ecological and evolutionary implications. We review evidence supporting this

conception and argue that broader appreciation of it will enrich the understanding of plant function and adaptation. We focus on angiosperm flowers and inflorescences, as they have received considerable recent attention, and their spatial and temporal variation directly affects plant fitness. Nevertheless, general conclusions arising from this examination also apply to vegetative structures and other metameric taxa. The conception of and evidence for plant phenotypes as dynamic mosaics has been developing for more than a century (see Schleiden, 1848). However, this perspective has not previously been elaborated as an articulated argument outlining facets of dynamic mosaic phenotypes, from measurement to diversification.

### Angiosperm phenotypes are mosaics

Metameric structure and pluripotent meristems allow plants to produce multiple reproductive organs, either individually or aggregated into inflorescences. If organs differ within a plant and function interactively, division of reproduction over plant bodies creates a phenotypic and functional mosaic. The mosaic nature of the reproductive phenotype is obvious for plants with qualitatively different flowers, such as Asteraceae with radiate inflorescences (Fig. 1d; Harris, 1999), species with sterile peripheral flowers in inflorescences (Fig. 1g,i; Morales *et al.*, 2013; Park *et al.*, 2019), those with hermaphroditic sexual systems involving mixtures of bisexual, female and/or male flowers (Fig. 1d,j; Diggle, 2003; Torices *et al.*, 2011; Tomaszewski *et al.*, 2018), and species with different fruit types (Imbert, 2002). More common, but less apparent, is quantitative variation among flowers of individual plants (Diggle, 2003; Herrera, 2009). Importantly, many quantitative traits vary systematically with flower position within inflorescences, including flower size, pollen and/or ovule number, and aspects of flowering phenology (Diggle, 2003; Ishii & Harder, 2012: Figs 1e,j,l, 2). Systematic variation must arise from corresponding developmental variation, rather than developmental instability.

Two nonexclusive processes can generate systematic variation within inflorescences: plasticity induced by resource competition, and position-dependent effects (Diggle, 1995, 2003). Resource competition occurs when development of early flowers or fruits usurps resources needed by later flowers and fruits (e.g. Ladio & Aizen, 1999; Kliber & Eckert, 2004; Torices & Méndez, 2010). As anthesis usually follows an ordered sequence within and among inflorescences, competition could generate systematic gradients in flower, fruit and seed traits. However, within-inflorescence gradients in floral traits commonly persist if competition is precluded by preventing pollination of early flowers (reviewed by Diggle, 1995, 2003). This persistence demonstrates that a flower's characteristics can depend on its absolute position in the inflorescence, in addition to its position (and development time) relative to competing flowers. Diggle (1995) called such position dependence an architectural effect.

The mosaic nature of plant phenotypes determines their environmental interaction and how their function and adaptation should be conceived and analysed. Just as a mosaic image cannot be appreciated fully by focusing on individual tiles, an individual leaf

or flower or even the average leaf or flower provides a limited view of a plant's phenotype and selection on its performance (Harder *et al.*, 2004; Herrera, 2009, 2017; Kulbaba *et al.*, 2017). Because of within-individual heterogeneity, trait variance is characteristic of plant phenotypes (Herrera, 2009). Furthermore, if traits vary systematically within plants, the variation pattern is also an essential phenotype characteristic (Kulbaba *et al.*, 2017). Given these features, performance and selection depend on the aggregate characteristics of an individual's phenotype, which is an emergent, synergistic property of the attributes and coordination of its individual organs.

### Angiosperm phenotypes are dynamic

The dynamics of angiosperm phenotypes involves three hierarchical components: continuous development of individual organs from initial primordium to abscission; sequential production of organs within and among branches, inflorescences and ramets during growing/reproductive seasons; and, for perennials, changes in organ production among seasons. For example, consider the life of an individual protandrous flower (Figs 1a,b,e,f, 3). Being itself a developmental and functional mosaic, a flower typically comprises four organ whorls: a basal calyx (sterile), followed proximally by the corolla (sterile), androecium (fertile) and gynoecium (fertile). Each whorl has its own developmental sequences and functional schedules. All whorls are initiated and begin developing relatively simultaneously, but only the calyx interacts with the environment during the bud stage, providing protection. At anthesis, the corolla opens by rapid cell expansion and mediates pollination (perhaps with the calyx). During the initial male phase, the anthers dehisce, often sequentially (Fig. 1a,e), loading pollen onto pollen vectors, and then stamens wilt (Fig. 1a) and perhaps abscise owing to programmed cell death. Female phase follows when the stigma(s) becomes receptive to pollen receipt and germination, often enlarging (Fig. 1b). During flowering stage the corolla may continue growing slowly and stamen and/or pistil growth or movement may position anthers and stigmas suitably for pollen exchange and to reduce sexual interference (Fig. 1a,b; Ruan & Teixeira da Silva, 2011). Flowering stage concludes when programmed cell death terminates stigma receptivity and the corolla wilts or abscises. The ovary now grows rapidly, as endosperms draw resources, embryos grow and tissues elaborate to form the fruit. Fruit development ends with dehiscence or dispersal, perhaps aided by a vector. For multiflowered species, these events typically occur in a staggered manner among flowers and fruits (Fig. 1c,e,f), often as the inflorescence expands. Therefore, a plant's reproductive season involves continual development, often in direct aid of floral function.

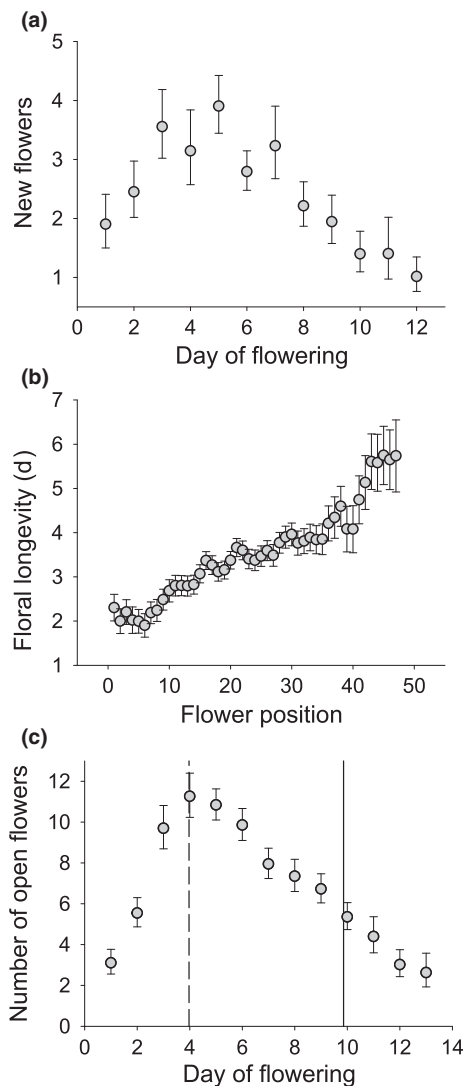
Inflorescence and infructescence traits illustrate additional temporal features of reproductive phenotypes (Harder & Prusinkiewicz, 2013). The numbers of flowers and ripe fruits that a plant displays simultaneously (display size) and the duration of its reproductive season are emergent properties of more elemental developmental traits (Meagher & Delph, 2001; Aizen, 2003; Harder & Johnson, 2005). Specifically, display sizes depend on 'birth' and 'death' rates, like the size of any population, and season



**Fig. 1** Examples of mosaic and dynamic features of the reproductive phenotypes of angiosperms. Panels (a–c) illustrate bumble-bee pollinated *Delphinium glaucum*, including: (a) a male-phase and (b) a female-phase flower (lower petals removed to expose undehisced (U), dehisced (D) and spent (S) anthers in (a) and styles (S) in (b)); and (c) a raceme with lower, older female-phase and upper, younger male-phase flowers. Many floral traits, including phenotypic gender, vary with flower position in this species (Ishii & Harder, 2012). Also note in (a) that only stamens with dehiscent anthers are vertical, positioning pollen at the mouth of the nectar spur (white petals), and that the styles and stigmas are not apparent; whereas in (b) stamens have wilted or abscised and the styles have elongated. In (c) the nectar spur (N) and lower sepal (S) are identified for one flower. Panel (d) shows a raceme of hummingbird-pollinated *Delphinium cardinale*, which differs from bee-pollinated delphiniums in that flowers open simultaneously and proceed relatively synchronously through male- and female-phases (Harder *et al.*, 2004). Panel (e) illustrates staggered flowering and anther dehiscence (U, undehisced; D, dehisced) in an *Allium mongolicum* inflorescence. Panels (f–j) illustrate qualitatively different flower types within inflorescences, including: (f) female ray flowers (F) and bisexual disc flowers (B, note dark anthers) of *Ligularia przewalskii*; (g) small central fertile flowers and large peripheral sterile flowers of *Hydrangea serrata*; (h) young yellow flowers with receptive stigmas and polleniferous anthers, and postpollination orange flowers of *Lantana camara*; (i) dark fertile flowers and pale sterile flowers of *Muscari armeniacum*; and (j) bisexual (B, note projecting styles) and male (M) flowers of *Anticlea occidentalis*. In addition to their qualitative differences, bisexual and male *A. occidentalis* flowers differ in size, and bisexual flowers also vary in size with flower position (Tomaszewski *et al.*, 2018). (k) Illustrates the floral display of *Satyrium longicauda*, the size of which varies with pollinator visitation owing to pollination sensitivity of floral longevity (Harder & Johnson, 2005). Panel (l) illustrates systematic within-flower petal-size variation and within-inflorescence flower-size variation of *Anthriscus sylvestris*.

duration additionally depends on total bud number. Thus, the number of new flowers opened per day (anthesis rate) and floral longevity determine floral display size per inflorescence. Correspondingly, a ramet's or genet's display size depends respectively on the daily numbers of newly flowering inflorescences and ramets. Consequently, a plant's display size varies, unless all flowers open

simultaneously and have identical longevity. Display size dynamics are further modified if anthesis rate and/or floral longevity vary among flowers (e.g. Figs 1k, 2) and bud number varies among inflorescences and ramets. Being emergent properties, display size and reproductive-season duration can be modified by temperature, pollination and resources, etc., or by selection that alters flower



**Fig. 2** Variation in mean ( $\pm$  SE) (a) number of new flowers per day (anthesis rate), (b) floral longevity, and (c) floral display size for racemes of 29 *Oxytropis splendens* Douglas plants. In (a–c), inflorescences opened their first flowers on Day 1, and in (b) flower position is numbered from the bottom to the top flowers. Flowers open from bottom to top, so flowers that open later are more distal on the inflorescence. In (c) the dashed and solid vertical lines indicate the mean days when the first flowers began wilting and the last flower buds opened, respectively. Based on Gallwey (2011).

birth or death rates (Meagher & Delph, 2001; Harder & Johnson, 2005; Gallwey, 2011). Although floral longevity (Ashman, 2004) and fruit ripening (Seymour *et al.*, 2013) are well studied from the perspective of individual organs, their consequences for floral and fruit display size remain largely unexplored. Even less is known about the controls and consequences of floral anthesis rate.

Given its dynamic nature, when is a flower ‘mature’? Two relatively abrupt events punctuate a flower’s continuous development: perianth expansion (anthesis) marks the transition from bud to flower stage; and perianth abscission denotes the shift from flower to fruit stages, if development continues. The different physiology, form and functions of each stage foster recognition and analysis of buds, flowers and fruits as distinct entities. However, the

implication that reproductive phenotype is static during each state, as implied by calling a bud, flower or fruit ‘mature’ is misleading. At no stage is a flower’s biochemistry, physiology or morphology static. Similarly, flower and fruit display sizes change continuously during a reproductive period (e.g. Fig. 2c). Consequently, no instant during a plant’s reproductive season, or indeed its life, adequately represents an individual’s phenotype. Instead, angiosperm phenotypes include the developmental and phenological components that govern the continual development and coordination of reproduction (also see Diggle, 1993; Minelli, 2018).

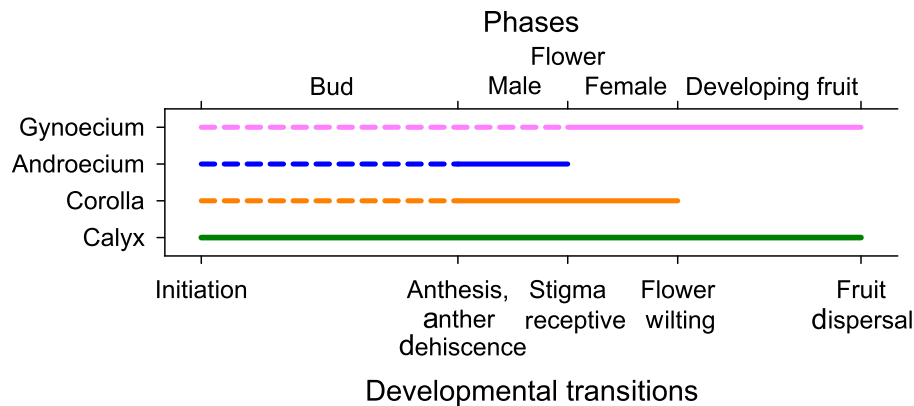
### Is an expanded phenotypic conception needed and tractable?

Conception of plant phenotypes as dynamic mosaics is warranted if it reveals unappreciated features of phenotypes, their development, functions and evolution and is amenable to analysis. We now address five questions concerning these requirements. How can dynamic mosaics be characterised and represented in analyses of phenotype function and adaptation? How is the development of dynamic mosaics controlled? Does the dynamic mosaic fundamentally affect plant performance? If so, is the spatial–temporal continuum amenable to natural selection? Finally, how do dynamic mosaic phenotypes evolve and contribute to angiosperm diversity?

#### Measurement and analysis

Unlike unitary traits, such as a seed’s mass, a single (scalar) measurement cannot represent an individual’s phenotype for traits that vary among repeated parts (organs within flowers, flowers, inflorescences, ramets) and/or through time (Diggle, 2014). Relevant measurements depend on the nature of intraindividual variation. In general, such variation can be represented by a trait’s mean and variance, both of which can be included in statistical analysis as a multivariate dependent or independent variable (Herrera, 2009). However, if the phenotype varies systematically on plant bodies or through time, trait variation is better viewed as functions of space and/or time (Kingsolver *et al.*, 2001; Kulbaba *et al.*, 2017; Gomulkiewicz *et al.*, 2018). Basic representation of such function-valued traits involves two vectors: one recording the spatial or temporal positions of an individual’s measurements,  $P$ , and the other recording the corresponding metric values,  $Z$ , of those measurements. This information is then used to characterise a function summarising individual’s trait variation. If the relation of  $Z$  to  $P$  is described adequately by parametric linear or nonlinear regression, the set of parameter estimates (e.g. mean and slope for linear regression) and residual variation could be used to represent an individual’s phenotype (parameters-as-data approach: Kulbaba *et al.*, 2017). For more complex relations, a spline function of an individual’s metric to position variables can be used as its phenotypic representation (Fig. 4a) (functions-as-data approach; Kulbaba *et al.*, 2017; Gomulkiewicz *et al.*, 2018).

The functions-as-data approach underlies functional data analysis, a relatively new body of statistical methods (Ramsay & Silverman, 2005; Wang *et al.*, 2016) relevant for analysing



**Fig. 3** Phenologies of the four whorls during the life of a protandrous flower. Solid lines indicate periods when organs interact with the environment that generally include active development (including programmed cell death), whereas dashed lines identify periods of development, but no ecological function.

function-valued traits (Kulbaba *et al.*, 2017). We briefly describe two such methods pertinent to regression analysis (Morris, 2015), which we illustrate with within-inflorescence floral variation of *Delphinium glaucum* (Ranunculaceae; Fig. 1c). The lengths of a lower sepal and the nectar spur were measured for seven, equally spaced flowers per inflorescence. Therefore, the measurement for flower  $j$  of plant  $i$  is the metric variable,  $z_{ij}$ , and flower position is  $p_j$  (numbered from bottom to top). Correspondingly, the measurements for subject  $i$  can be represented functionally as  $z_{ij} = f_i(p_j) + \varepsilon_{ij}$ , where  $f_i(p_j)$  denotes the function's value for the trait at  $p_j$  and  $\varepsilon_{ij}$  is the difference of  $z_{ij}$  from its functional representation,  $f_i(p_j)$ . We characterised  $f_i(p_j)$  as a spline (e.g. Fig. 4a), which is a connected set of polynomial regressions defined along consecutive intervals of  $P$  (Ramsay & Silverman, 2005).

Function-on-scalar regression (FOSR) is used to assess effects of one or more continuous scalar independent variables on a function-valued dependent variable. For example, consider the effect of basal stem diameter ( $x_i$ , scalar independent variable) on spline functions of within-inflorescence variation in nectar-spur length ( $f_i(p_j)$ : functional dependent variable) for 57 *D. glaucum* plants. For an independent variable to predict variation of a function of spatial or temporal position among individuals, both the intercept and associated (partial) regression coefficient must also be functions of position,  $\beta_0(p_j)$  and  $\beta_1(p_j)$  respectively. Therefore, the linear regression model for the estimated effect of a single independent variable,  $X$ , on the function-valued trait of individual  $i$  is

$$\hat{f}_i(p_j) = \beta_0(p_j) + \beta_1(p_j)x_i.$$

The fitted functional regression coefficient,  $\beta_1(p_j)$ , for the *D. glaucum* example (Fig. 4c) identifies a negative effect of stem diameter on spur length for basal flowers (relative flower position,  $P < 2$ ), but a generally positive effect for more distal flowers. Statistical significance of these effects is evident at positions for which the observed  $F$ -test function comparing the estimated regression function to 0 (e.g. blue curve in Fig. 4d) exceeds  $> 95\%$  of  $F$ -test functions based on random permutations of the observations that disrupt systematic within-individual variation

(e.g. grey curves in Fig. 4d). Based on this approach, the stem-diameter effect for *D. glaucum* is significantly negative for flowers at positions  $P < 1.7$  and significantly positive for  $2.7 < P < 5.6$  and  $P > 6.6$ . These results reveal heterogeneous effects of plant size on the spatial mosaic of inflorescences that traditional statistical methods cannot detect.

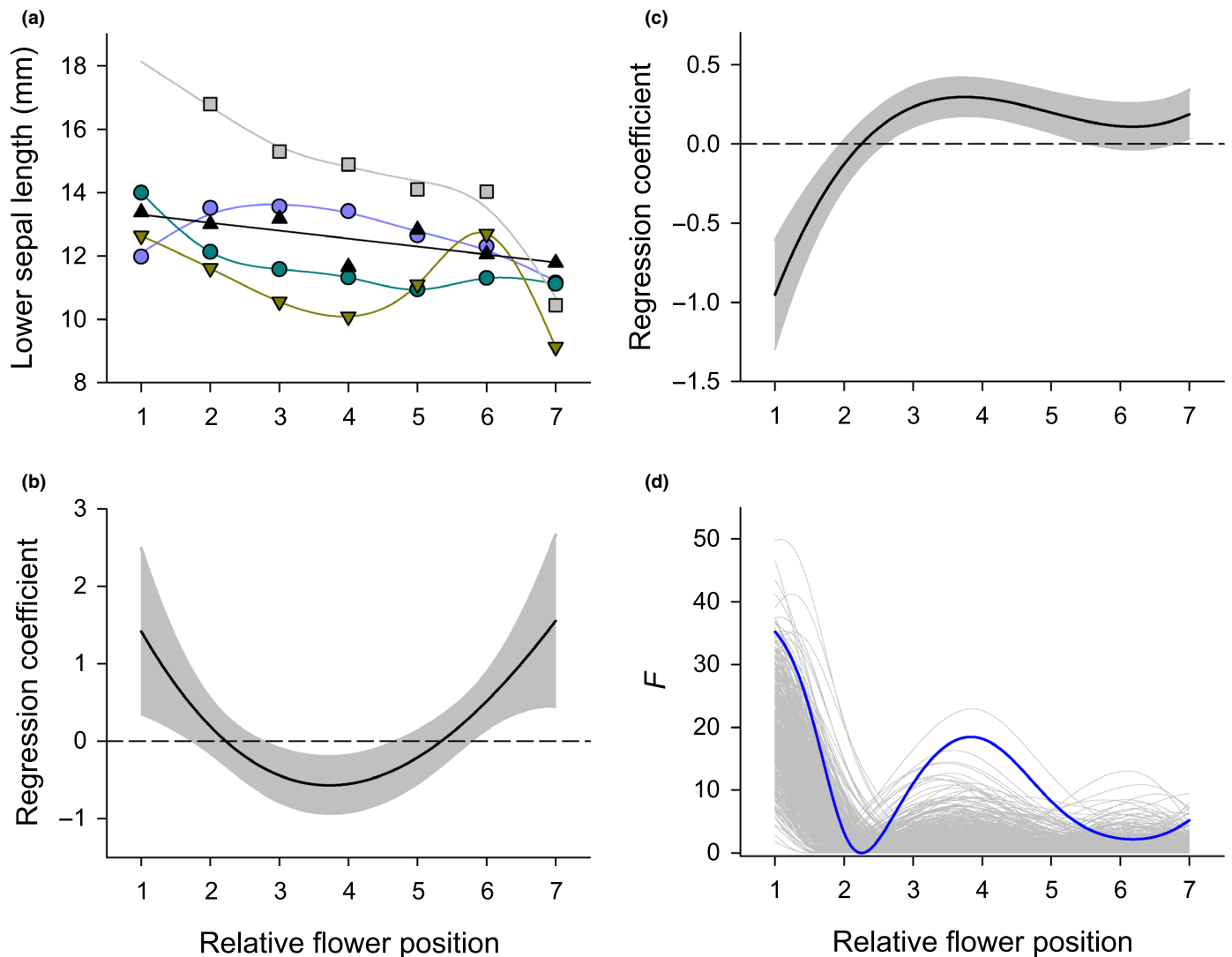
Scalar-on-function regression (SOFR) is used to assess the effects of function-valued (and scalar) independent variables on a scalar-dependent variable,  $Y$ . To illustrate, consider the effect of within-inflorescence variation in the length of the showy lower sepals ( $f_i(p_j)$ : functional independent variable) on overall fruit production per plant ( $y_i$ ) for 64 *D. glaucum* plants. For this simple case with a single, function-valued independent variable the linear regression model is

$$\hat{y}_i = \beta_0 + \int_0^P \beta_1(p)f_i(p)dp.$$

The second term represents the integrated effect on the dependent variable of within-individual variation in the functional independent variable over all positions. As this integrated effect is a single value for each individual, only a scalar intercept ( $\beta_0$ ) is needed and a single statistical test can be applied. For the *D. glaucum* example illustrated in Fig. 4b,  $\chi^2 = 9.71$  (3 df,  $P < 0.025$ ). This analysis detected higher fruit production by plants with relatively long lower sepals on the bottom and top flowers within inflorescences but relatively short lower sepals on middle flowers. These results expose differential effects of the spatial mosaic of inflorescences on overall female reproductive success that elude traditional statistical analysis.

### Developmental control

The dynamic mosaic nature of plant phenotypes reflects the primacy of development (broadly construed) in organising and maintaining metameric plant bodies. Dynamics arise straightforwardly from serial initiation and development of individual metamers (Reeves *et al.*, 2012). Serial initiation also influences the instantaneous mosaic character of plants, if organs differ in their



**Fig. 4** Examples of functional data analysis of within-inflorescence variation for *Delphinium glaucum*, including (a) representation of observed (symbols) variation of lower sepal length (labelled *S* in Fig. 1c) with spline functions (curves) for six plants, (b) scalar-on-function regression (SOFR) of the effect of variation in lower sepal length on overall fruit number, and (c, d) function-on-scalar regression (FOSR) of the relation of variation in flower spur length (labelled *n* in Fig. 1c) to basal stem diameter. Panel (b) illustrates within-inflorescence variation of the estimated SOFR regression coefficient function ( $\pm$  95% confidence interval (grey band) for 64 inflorescences: the dashed horizontal line identifies no effect. Panels (c and d) respectively depict within-inflorescence variation of the estimated FOSR regression coefficient function ( $\pm$  95% confidence interval) and the associated observed (blue line) and permutation (grey lines) *F*-test functions for 57 inflorescences.

developmental stages. Relevant mosaic features therefore depend on the relative timing of development of an individual's organs and its control. Less straightforward is the generation of differences among organs at the same stage. As a plant's cells are genetically identical (barring somatic mutation), such heterogeneity could reflect developmental instability (Møller & Shykoff, 1999) and/or developmental plasticity (Gaillochet & Lohmann, 2015). However, only developmental plasticity can generate systematic trait variation within individuals, so we focus on it here.

Although a plant's cells all use the same instruction manual encoded in their genes, the manual is implemented selectively and with different emphases during development. Differential development within plant bodies is evident in the morphological and physiological variety of tissue and organ types and variation within

types. Developmental plasticity is well studied in the context of phenotypic plasticity, whereby an individual's conditions alter its development, generating quantitatively (reaction norms) or qualitatively (polyphenism) different phenotypes (Gilbert & Epel, 2009). Owing to the metameric structure and indeterminate assembly of plant bodies, phenotypic plasticity can contribute significantly to the dynamic, mosaic nature of their phenotypes (de Kroon *et al.*, 2005), and their ability to contend with environmental heterogeneity. Obvious examples involve phenotypic effects of among- and within-plant variation in nutrient availability including systematic variation among flowers and fruits (Diggle, 1995; Camargo *et al.*, 2017; Spigler & Woodard, 2019). Less obvious, but equally relevant, are floral and inflorescence responses to inadequate pollination, including extended floral longevity,

increased flower production and floral display size, modified plant gender, increased production of cleistogamous flowers, and breakdown of self-incompatibility (Lawrence, 1993; Diggle, 1994; van Doorn, 1997; Vogler *et al.*, 1998; Harder & Johnson, 2005; Albert *et al.*, 2011; Fig. 1k).

Phenotypic plasticity requires coordinated, differential regulation of gene expression. Gene regulation is complex (Minelli, 2018) and largely beyond the scope of our review. However, the roles of various signalling molecules warrant mention. Signalling molecules are synthesised in different locations (tissues) from their site of action and so must be transported from cell to cell or via the vascular system (Lough & Lucas, 2006; Park *et al.*, 2017). Because they act at a distance, signalling molecules convey information about the state of the synthesis site to the target cells, possibly altering their gene expression. For example, seasonal change in photoperiod activates the *FLOWERING LOCUS T* gene in *Arabidopsis* leaves but the resulting protein, florigen, acts on the distant shoot apical meristem (SAM) after transport in phloem (Corbesier *et al.*, 2007). Florigen induces a switch to floral identity in the SAM, which then generates a reproductive rather than vegetative axis (Corbesier *et al.*, 2007). It also mediates differential flowering by apical and axillary meristems, influencing inflorescence architecture (Shalit *et al.*, 2009). Signalling molecules include various macromolecules, microRNA and, importantly, hormones (Lough & Lucas, 2006; Park *et al.*, 2017). Hormones play central roles in coordinating gene expression and growth within and among ramets (Alpert *et al.*, 2002; Hill, 2015; Runions *et al.*, 2015). Through their actions, hormones mediate development (Chandler, 2011; Diggle *et al.*, 2011; Han *et al.*, 2014), including phenotypic plasticity (Farnsworth, 2004; Gaillochet & Lohmann, 2015; Hill, 2015).

Unlike phenotypic plasticity, the developmental plasticity that generates architectural effects depends on an organ's absolute position on the plant body (Diggle, 1995). Developmental regulation of architectural effects has received little specific attention. However, as for phenotypic plasticity, mediation of differential gene expression by hormone gradients seems likely (Diggle, 2014). For example, temporal auxin gradients in capitula of *Tripleurospermum* (syn. *Matricaria*) *inodora* (Asteraceae) control differential expression of two floral-meristem identity genes, generating morphologically distinct outer ray florets (pistillate, zygomorphic) and inner disc florets (bisexual, actinomorphic; Zoulias *et al.*, 2019). Gradient control of genes with quantitative effects could similarly generate the systematic variation of continuous traits that characterises architectural effects.

If temporal and spatial within-individual variation arise from control of gene expression, does this control vary genetically among individuals, as is required for variation patterns to respond to natural selection? Studies comparing clonal replicates in different environments detected significant among-genet variation for within-individual variation in inflorescence characteristics, including architectural effects (Diggle, 1993; Grimplet *et al.*, 2019). Moreover, Grimplet *et al.* (2019) found among-genet variation in hormone concentrations and that phenotypic variation of mosaic traits paralleled gibberellin variation. Using SNP-based estimates of relatedness coupled with parameters-as-data characterisation of

within-individual variation (see the 'Measurement and analysis' subsection), Kulbaba *et al.* (2017) detected significant narrow-sense heritability for declining anthesis rate within *Delphinium glaucum* inflorescences. These results demonstrate that within-individual variation can differ genetically among genets, rather than simply being environmentally determined, and could be modified by natural selection.

### Functional significance

Being immobile, plants must contend with environmental uncertainty at their establishment site and variable conditions for growth and reproduction during their lives. How individuals can best contend with environmental variation depends on its scale. Short-term environmental variation is best accommodated by physiological flexibility. Site uncertainty and unpredictable variation on a timescale that allows the production of new metamers can also be mitigated by individual and within-individual anatomical/morphological plasticity, respectively. Both physiological flexibility and morphological plasticity are suitable responses to stochastic environmental change. If instead the environment varies predictably, systematic within-individual variation, including architectural effects, is advantageous. Unlike the preceding phenotypic responses, such phenotypic variation is produced in anticipation of consistent environmental heterogeneity. As systematic within-individual variation is a fundamental feature of dynamic mosaic plant phenotypes, we focus specifically on its functions.

Dynamic and mosaic features of plant phenotypes can provide at least four nonexclusive benefits for reproduction.

**Functional ontogeny** As fitness is a lifetime characteristic, selection optimises individual function during all life stages for all organisms (Werner & Gilliam, 1984; Donohue, 2014), often emphasising different functions during the lifecycle (for example grow when young, reproduce later). Therefore, ontogeny simultaneously alters phenotype and function. For metameric organisms, repeated, ongoing initiation, development and senescence of individual structures generates constant flux in their specific functions and in the mixture of functions in which an organism engages simultaneously. For example, consider postflowering development of vertebrate-dispersed fruits, as illustrated by tomato (Tohge *et al.*, 2014). Initially, fruits are green with relatively high concentrations of defensive secondary compounds. Therefore, they can photosynthesise, partially supporting seed development, are relatively cryptic in the surrounding vegetation, and are somewhat defended against predispersal predation. As seeds mature, auxin concentration in enclosing fruit tissue declines, stimulating increased ethylene production and sensitivity (Shin *et al.*, 2019). These hormonal shifts induce fruit colour change, reduced concentrations of defensive compounds and increased sugar concentrations, rendering fruits more apparent and desirable to dispersal agents. As tomato plants produce inflorescences and flowers within inflorescences sequentially (Park *et al.*, 2012), the number and proportions of fruits involved in photosynthesis, defence and attraction of dispersal agents also change continuously during a plant's fruiting period. All features of this dynamic

promote seed development and dispersal (in nonagricultural situations). Such functional ontogeny is also evident in other aspects of reproductive phenotypes, including dichogamy and floral colour change, as mentioned below.

**Mating efficiency** Another advantage of dynamic reproductive phenotypes arises if mating opportunities vary systematically during a plant's flowering period. Such variation could arise from changes in the availability of mates, competitors and/or pollinators that affect pollination success and self-pollination vs cross-pollination (Aizen, 2001; Ison *et al.*, 2014; Yin *et al.*, 2016). Given consistent variation in mating opportunities, displaying a fixed number of flowers daily during the flowering period is likely to be detrimental. Instead, large displays enhance attraction when pollinators visit infrequently, whereas small displays are better when pollinators visit often, because of reduced among-flower self-pollination (geitonogamy) and associated pollen discounting (see Harder & Johnson, 2005). Therefore, systematic temporal variation in mating conditions favours dynamic variation in anthesis rate, floral longevity and inflorescence display size (e.g. Fig. 2). Similarly, population-level changes in floral sex ratio associated with dichogamy or monoecy favour increased female investment when male flowers (and female mating opportunities) dominate, but emphasis on male function when female flowers dominate (Brunet & Charlesworth, 1995; Brookes & Jesson, 2010; Ishii & Harder, 2012). As the roles and vulnerability of organs and ecological opportunities are likely to vary temporally for all plant species, dynamic phenotypes should be the rule, rather than the exception.

**Division of labour** Production of multiple organ copies within flowers, multiple flowers within inflorescences and multiple ramets per genet, perhaps coupled with functional ontogeny, allows functional specialisation and/or reduced mating interference among reproductive structures, promoting a genet's overall reproductive success. Adaptive division of labour is evident for mosaics of qualitatively different flowers. Production of sterile peripheral flowers (e.g. Fig. 1g,i; Morales *et al.*, 2013; Park *et al.*, 2019) and retention of showy perianths that change colour after flowers cease receiving pollen (e.g. Fig. 1h; Weiss & Lamont, 1997; Brito *et al.*, 2015) generally enhance pollinator attraction, without increasing geitonogamy. Many features of mosaic phenotypes implement division of labour, including production of distinct feeding and pollinating anthers within flowers (heteranthery, Vallejo-Marín *et al.*, 2009), segregated presentation of female(-phase) and male(-phase) flowers within inflorescences (Fig. 1c,f; Harder *et al.*, 2000; Tomaszewski *et al.*, 2018), and production of separate vegetative and reproductive ramets (Charpentier & Stuefer, 1999).

**Resource efficiency** This benefit of within-individual variation arises from resource consequences of mating efficiency and division of labour. Sequential anthesis and pollination of flowers within inflorescences often establishes a parallel gradient in fruit development and resource demand by individual fruits. Accompanying resource competition that consistently reduces fruit set or

proportional seed success in later fruits (Stephenson, 1981) favours greater emphasis on female function of early flowers (e.g. more ovules) and on male function of late flowers (e.g. ovary abortion). This association of systematic gender variation with flowering sequence within inflorescences is expected from both mating and resource efficiency, so they should synergistically promote this common pattern of within-individual variation (Austen *et al.*, 2015). Resource efficiency is also evident in size-dependent gender variation among plants. For example, in *Sagittaria latifolia* (Sarkissian *et al.*, 2001) and *Anticlea occidentalis* (Fig. 1j; Tomaszewski *et al.*, 2018) average production of female and bisexual flowers, respectively, increases with plant size, whereas that of male flowers does not vary.

This overview demonstrates some of the diverse complementary benefits of systematic within-individual variation. With respect to reproduction, these benefits arise from mating quantity and quality and the resource economy of fruit and flower production. Whether such variation is favoured depends on its benefits and costs. For example, floral traits that influence pollen exchange with pollinators should vary little within and among plants, because of the benefits of consistent pollen placement on pollinators' bodies (Diggle, 2014). Nevertheless, the prevalence of systematic temporal and spatial within-individual variation, including architectural effects, among angiosperms indicates widespread benefits of dynamic, mosaic phenotypes.

## Selection

If dynamic mosaic phenotypes promote individual performance (see the 'Functional significance' subsection) and are heritable (see the 'Developmental control' subsection), their characteristics will evolve by natural selection. We now address two aspects of this selection: evidence for relevant phenotypic selection, and particular features of selection that might shape adaptation of dynamic mosaic phenotypes.

Past studies of phenotypic selection on reproductive traits largely adopted the flower-centred (floricentric; Harder *et al.*, 2004) perspective (e.g. Stebbins, 1950) that has dominated the analysis of plant reproduction for over two centuries. For example, all 56 studies of phenotypic selection on reproductive traits reviewed by Harder & Johnson (2009) considered the traits of one or the average flower per plant and only 20 studies considered basic aspects of the reproductive mosaic, such as total flower number or the number of open flowers. Only 29% of the 386 selection gradients for floral traits estimated by these studies detected significant selection. Harder & Johnson (2009) suggested that this relatively low frequency could arise if phenotypic selection is typically studied during periods of evolutionary stasis, when selection on floral traits is weak and inconsistent. Our conception of phenotypic characteristics suggests the additional possibility that floricentric analysis provides an incomplete perspective on selection of inherently dynamic, mosaic phenotypes.

Herrera's (2009) analyses of phenotypic selection on within-individual variation first demonstrated this possibility. He studied 10 floral traits for six species, simultaneously estimating selection gradients for trait means and within-plant variances (see the



‘Measurement and analysis’ subsection). All 10 analyses that included trait variances detected significant selection compared with significant selection for only five analyses that considered the mean alone (also see Palacio *et al.*, 2016; Arceo-Gómez *et al.*, 2017). The contrasts of selection on mean vs variance and of these results with the low evidence of selection detected by previous phenotypic-selection studies signal that selection acts more pervasively on the reproductive mosaic of angiosperms than on features of individual or ‘typical’ flowers.

The nature of phenotypic selection could be even more intriguing than Herrera’s study illustrates, as he did not consider selection on systematic and dynamic aspects of within-individual variation. Phenotypic selection on these features can be assessed by treating them as function-valued traits (e.g. Fig. 4a) that are then included as independent variables in regressions of variation in plant performance (see the ‘Measurement and analysis’ subsection; Kulbaba *et al.*, 2017). For example, Fig. 4(b) illustrates phenotypic selection on within-inflorescence variation of lower sepal length for *Delphinium glaucum* (see Fig. 1c), as detected by SOFR. This analysis revealed heterogeneous selection within inflorescences, being positive for bottom and top flowers, but negative for middle flowers. Furthermore, this regression model described variation in fruit set better than models that included only the trait mean (floricentric perspective) or the mean and variance (Herrera approach) for individual plants (Clocher, 2017). Such results demonstrate phenotypic selection on systematic within-individual variation that could modify variation patterns, if they are heritable.

Two aspects of selection are especially pertinent to adaptation of systematic within-individual variation. First, phenotype development imposes serial dependence among phases within organs and among sequential organs owing to pleiotropy (Donohue, 2014; Smith, 2016), or allocation constraint (Lloyd, 1980; Ashman & Schoen, 1997; Torices & Méndez, 2010). Serial dependence creates correlations of the same trait at different times (see Donohue, 2014), and of different floral, fruit, seed or inflorescence traits (e.g. Routley & Husband, 2005; Sargent *et al.*, 2007). On the one hand, events early in the lives of reproductive structures (e.g. number of ovules initiated) can establish the capacity for later events (e.g. seed production: Lloyd, 1980). On the other hand, characteristics of late stages may determine adaptive options for characteristics of earlier stages. For instance, selection of small flowers that facilitate pollination by wind or small insects may be enabled by initiation of few ovules in flower buds. In either case, the response to selection on a feature of one reproductive stage will depend on correlated consequences for other stages (e.g. Routley & Husband, 2005). Therefore, selection should favour coordinated development of buds, flowers, fruits and inflorescences, which may generate outcomes different from those expected from direct selection on the focal stage. Furthermore, because of serial dependence, morphological evolution of plant reproductive organs should commonly involve heterochrony, or change in temporal aspects of development; specifically rate and timing (see Li & Johnston, 2000; Buendía-Monreal & Gillmor, 2018; Box 1).

The second feature, genetic accommodation, relates to selection on mosaic variation. We explain accommodation with respect to the evolution of architectural effects, but it applies also to

phenotype dynamics. Architectural effects could evolve via genetic accommodation if chronically poor success of reproductive organs at some positions on plant bodies favours genetically regulated gradients in flower/fruit development (Brunet & Charlesworth, 1995; Diggle, 2003; Diggle & Miller, 2013). Variable success can be an intrinsic feature of the structure of plant bodies, depending on the proximity of organs to vegetative resource sources along branches and the relative timing of their resource demand. Chronic variation could also arise from structured environmental interaction, such as that generated by seasonal dynamics of pollinator phenology or population floral sex ratio (e.g. Aizen, 2001). In either case, individuals whose phenotypic variation promotes reproductive performance compared with that of individuals with other variation patterns should generally produce more offspring. The appropriate variation pattern could arise from phenotypic plasticity or architectural effects. However, architectural effects are likely to contend with predictable intrinsic or extrinsic environmental variation more efficiently (Diggle & Miller, 2013). If so, architectural effects could arise as consistent selection transfers control of within-individual variation from phenotypic plasticity to genetically based regulation of gene-expression gradients over generations (see Diggle & Miller, 2013; Ehrenreich & Pfennig, 2015). Nevertheless, retention of some phenotypic plasticity, in addition to architectural effects, should often help to mitigate unpredictable environmental variation. Therefore, dynamic phenotypic mosaics should commonly incorporate both architectural effects and phenotypic plasticity, as is commonly observed (Diggle, 2003).

## Diversification

Angiosperm reproductive traits have diversified extensively as selection generated alternative solutions to plant immobility and reliance on pollen vectors for outcrossing. These solutions reflect opportunities and limitations afforded by metameric plant bodies (e.g. Torices *et al.*, 2019), including the dynamic mosaic nature of reproductive phenotypes (see the ‘Functional significance’ subsection). Consequently, evolution of the dynamic mosaic is integral to angiosperm diversification. Dynamic diversity is evident in interspecific variation of flower development from bud to ripe fruit, floral longevity, inflorescence display size, and clonal dynamics (e.g. Bertin & Newman, 1993; Ashman, 2004; Harder *et al.*, 2004; see Fig. 1c,d). Mosaic diversity is also prevalent, most obviously for species in which individuals present several flower types (Renner & Ricklefs, 1995; Vallejo-Marín & Rausher, 2007; Mamut & Tan, 2014), or exhibit floral colour change (Weiss & Lamont, 1997). Differing systematic within-plant variation of floral traits is also known for > 28 families (Diggle, 2003 (based on contemporary taxonomy); Kulbaba *et al.*, 2017), which is doubtless a gross underestimate. Therefore, diversification of dynamic mosaic phenotypes is likely to be a pervasive, if poorly studied, component of the evolution of the remarkable reproductive variety of angiosperms.

Phenotypic diversification requires the alteration of underlying developmental programmes (Arthur, 2011; Minelli, 2018). Much within-individual variation is likely to have arisen from heritable gradients of signalling molecules that control developmental

**Box 1** Examples of the diversification of dynamic mosaics

In general, lineages diversify phenotypically as different populations adapt to contrasting local environmental conditions. Associated evolution of morphology involves one or more of four modes of developmental change. Here, we present examples of these modes that specifically demonstrate their relevance for the diversification of dynamic mosaic phenotypes.

**Heterochrony:** Changes in the relative onset, rate and/or termination of developmental processes commonly underlie plant trait diversification (Li & Johnston, 2000; Lemmon *et al.*, 2016; Buendía-Monreal & Gillmor, 2018), often as means of implementing changes in pollination systems (Armbruster *et al.*, 2013; Strelin *et al.*, 2018), mating systems (Li & Johnston, 2010) or sexual systems (Strittmatter *et al.*, 2008). Two examples specifically illustrate heterochronous diversification of dynamic mosaics. The first entailed abbreviated development of male flowers in monoecious inflorescences of some Madagascar *Dalechampia* species (Armbruster *et al.*, 2013). As a consequence, these flowers barely open, requiring pollen-collecting pollinators to vibrate male flowers to extract pollen. The evolution of the bud-like form of male, but not female, flowers altered the phenotypic mosaic and occurred in association with a pollinator transition from generalised pollen-feeding insects to pollen-collecting bees. The second example involves *Delphinium cardinale* (Fig. 1d), a derived hummingbird-pollinated species in a largely bumble-bee-pollinated clade (Harder *et al.*, 2004). Flowers of all *Delphinium* species are protandrous. In contrast with the staggered acropetal anthesis of bee-pollinated species, *D. cardinale* flowers open simultaneously and pass synchronously through male- and female-phases (e.g. Fig. 1c). These contrasting flowering patterns both limit geitonogamy because hummingbirds move upward less consistently than bumble-bee pollinators while feeding on vertical inflorescences (Harder *et al.*, 2004; also see Harder *et al.*, 2000). Together, these examples illustrate roles of heterochrony in diversification of mosaic and dynamic features of plant phenotypes, in the first case requiring modularity and in the second enhancing it.

**Heterotopy:** Spatial change in development seems most relevant to diversification of the mosaic character of plant phenotypes. Obvious examples include division of labour involving the same organ type within flowers or different flower types within inflorescences (see the 'Functional significance' subsection: Baum & Donoghue, 2002). Indeed, variation in division of labour, likely arising via heterotopy, is a central theme in the evolution of both hermaphroditic sexual systems that involve combinations of female, male and/or bisexual flowers (Torices & Anderberg, 2009; Bello *et al.*, 2013; Diggle & Miller, 2013) and pollination systems involving sterile peripheral flowers within inflorescences to enhance pollinator attraction (Donoghue *et al.*, 2004). That the necessary changes, such as arrest of gynoecium or androecium development (Diggle *et al.*, 2011), affect just a subset of a plant's flowers also provides clear evidence that modularity greatly facilitates the evolution of mosaic phenotypes by heterotopy.

**Heterometry:** Changes in the amount of gene products that regulate development are likely widely involved in diversification of dynamic mosaic phenotypes, as their existence requires such variation. Prusinkiewicz *et al.*'s (2007) theoretical model of diversification of inflorescence architecture is informative in this context. This model considers a temporal decline in the concentration of a hypothetical substance, *veg*, that controls the identity of individual meristems. Specifically, if  $veg > V$  a meristem in a developing inflorescence produces a vegetative metamer (shoot segment with associated meristem), whereas when *veg* falls below this threshold it produces a flower, which is a terminal fate. Given this criterion, the temporary difference in *veg* concentrations between the apical meristem,  $veg_A$  and its most recent daughter lateral meristem,  $veg_L$ , governs inflorescence architecture. Specifically,  $veg_L = veg_A$  generates a panicle,  $veg_L < veg_A$  generates a raceme, and  $veg_L > veg_A$  generates a cyme. A subsequent comparative transcriptome study of wild-type and mutant tomato lines and a wild relative with different inflorescence architectures detected contrasting temporally variable gene-expression patterns consistent with this model (Park *et al.*, 2012). These results illustrate that characteristic qualitative differences between species (in this case inflorescence architecture) can evolve by heterometric changes in the quantitative control of development. Such changes could also underlie diversification of continuous and discrete variation among flowers within inflorescences.

**Heterotopy:** Changes in transcription factors have been little studied in the context of within-individual variation, but a transition that occurred during the domestication of maize (Wang *et al.*, 2005) illustrates their relevance to mosaic diversification. In the wild progenitor of maize, a stony casing (cupule + glume) protects individual fruits (kernels) from damage during ingestion by mammalian seed dispersers. In maize, this structure is greatly reduced owing to substitution of a novel mutation at a single locus that encodes a transcription regulator. This genetic change reduces the stony casing to a remnant, making the kernel edible. Because this substitution affects female inflorescences, but not male inflorescences, heterotypic (and heterotopic) modification altered the mosaic phenotype in the maize lineage. Thus, heterotypic evolution of a mosaic phenotype enabled a major change in human diets.

heterogeneity (see the 'Developmental control' subsection), in which case diversification of dynamic mosaics requires gradient modification. Three features of developmental evolution seem germane: genetic accommodation in novel reproductive environments; developmental modularity; and modes of developmental modification. We addressed genetic accommodation above ('Selection'), so we consider only the latter two features here.

Developmental modularity arises from integration of networks of interacting processes that generate structures or biochemical products (Klingenberg, 2008). Modules exist because of their integration and need not correspond to a specific structure. Importantly, for metameric organisms, developmental module  $\neq$  metamer. For example, a network of

processes could govern gynoecium development of all a plant's flowers, integrating characteristics of multiple metamers. Because of integration, a module's features correlate strongly, so change in one process has multiple effects that can constrain module evolution. By contrast, traits of different modules often correlate weakly and are more amenable to independent evolution (Diggle, 2014). For phenotypic mosaics, modularity allows contrasting within-individual variation among modules. For example, gynoecium and androecium characteristics often vary differently with flower position within inflorescences, creating within-individual gender variation (Diggle, 2003; Ishii & Harder, 2012). Such module independence should facilitate diversification of phenotypic mosaics.

The evolution responsible for phenotypic diversification generally involves four nonexclusive modes of developmental change (Arthur, 2011): heterochrony – altered relative timing of developmental events; heterotopy – altered relative location of specific developmental events; heterometry – altered amount of gene product; and heterotypy – structural change of transcription-factor proteins involved in gene regulation. Despite limited studies of the development and evolution of within-individual variation, some evidence illustrates involvement of these evolutionary modes in the diversification of dynamic mosaic phenotypes (see e.g. Box 1). Given its temporal effects, heterochrony is obviously relevant to diversification of phenotype dynamics (e.g. see Harder *et al.*, 2004; Fig. 1c,d). Heterochrony may commonly underlie such diversification because many expressed genes exhibit age-dependent expression (Park *et al.*, 2012) and it adjusts developmental schedules, rather than rearranging ontogeny and disrupting modular integration (Gould, 2002). Similarly, heterotopy is obviously relevant to mosaic diversification, as it involves spatial changes in development. The metameric structure of plant bodies allows two types of heterotopy: within-structure heterotopy, such as conversion of protective sepals into attractive organs within flowers; and among-structure heterotopy, such as evolution of different flower types within or among inflorescences from ancestors with a single type. Therefore, heterotopy is likely to underlie diversification of division of labour within plant bodies (e.g. Donoghue *et al.*, 2004; Torices & Anderberg, 2009; Armbruster *et al.*, 2013; Diggle & Miller, 2013). Note that among-structure heterotopy will often involve differential implementation of other modes of developmental change, such as heterochrony, among metamers (e.g. Armbruster *et al.*, 2013). Fewer examples are evident for involvement of heterometry (perhaps Diggle & Miller, 2013) and heterotypy (Wang *et al.*, 2005) in diversification of dynamic mosaics, perhaps because they are more difficult to detect. Nevertheless, heterometry may frequently alter systematic within-individual variation, as both involve quantitative variation in the gene products that regulate development (see ‘Developmental control’). Importantly, heterometry generates interspecific allometry (Arthur, 2011), which is likely to feature often in the diversification of mosaic phenotypes.

This brief overview illustrates that the complete spectrum of modes of developmental evolution underlies diversification of dynamic mosaic phenotypes. Furthermore, these modes can be involved in various combinations (e.g. Armbruster *et al.*, 2013; Wang *et al.*, 2005). This interacting variety facilitates developmental modification, allowing dynamic mosaics to evolve and diversify in response to new environments. Indeed, many examples described in Box 1 are associated with transitions in pollination systems (e.g. Donoghue *et al.*, 2004; Harder *et al.*, 2004; Armbruster *et al.*, 2013; Strelin *et al.*, 2018) or sexual systems (e.g. Torices & Anderberg, 2009; Diggle & Miller, 2013), contributing broadly to diversification of angiosperm reproduction. The different modes of developmental change likely also underlie diversification of systematic within-individual variation, but this

influence attracts less attention than qualitative change than the evolution of distinct flower types.

## Conclusion

The evidence reviewed above illustrates clearly that, rather than static uniformity, plant phenotypes change continuously during their lives and include extensive, often systematic, within-individual variation. This dynamic mosaic can be heritable, affects plant function and is subject to phenotypic selection. Consequently, developmental, morphological, ecological and evolutionary analysis that ignores the dynamic mosaic character of plant phenotypes may often lead to incomplete or inaccurate conclusions. We specifically elaborated this perspective with respect to plant reproduction; however, vegetative structures are similarly dynamic and variable within individuals (Herrera, 2009). Therefore, the dynamic mosaic perspective applies broadly to plant phenotypes and should therefore be incorporated generally into the understanding of how phenotypes arise, function and evolve.





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## Author contributions

The perspective presented here developed over many years during two- and three-way discussions involving all authors. ICC conducted the research illustrated in Fig. 4. LDH drafted the manuscript and all authors participated in refining it to produce the final version.

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