Article Addendum

How little is too little?

The adaptive value of floral integration

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For more than a century the idea that natural selection favors high levels of floral integration has prevailed as a paradigm among floral biologists. However, there is very little empirical evidence of the adaptive value of floral integration. In this addendum we highlight an important result derived from an empirical study complemented with a literature review and mathematical simulations. Results indicated that intrafloral integration but not floral integration was selected among four species of Rosaceae. The literature review coupled with null models revealed that flowering plants have on average lower than expected levels of floral integration. Mathematical simulations further demonstrated that observed levels of floral integration might result from selection favoring increased intrafloral integration. Altogether, these findings suggest that in most flowering plants, floral integration has a low adaptive value and could be a by-product of selection favoring intrafloral integration.

To some extent all living organisms express some degree of phenotypic integration as the result of the coordinated functions that ensures life. Thus integration itself constitutes an adaptation intimately related with the evolution of life on earth. Although empirical evidence has reported the presence of variation in the magnitude of integration among families, species, populations and individuals, few studies have examined the adaptive value of this variation (Fig. 1A, B and D).1 Because integration is directly related with functionality, the magnitude of integration can have important consequences for the interaction between species and the environment.1, 2

In most species of Angiosperms, the flowers represent complex modular structures that evolved to ensure both reception and exportation of pollen via biotic pollination.3 Because this complex function requires the morphological and behavioral matching between plants and animal vectors, the idea that high levels of floral integration are favored by natural selection was put forward since the conception of evolutionary biology (Fig. 1A).3 This hypothesis was further developed by the establishment of the pollination syndrome concept: functional and morphological characteristics of the flower in relation with the type of animal pollinator.5 Moreover, Berg’s concept of correlation Pleiades synthesized Darwin’s ideas by postulating that, in order to ensure a correct matching between floral and pollinators morphology and behavior, species with highly specialized pollination systems should express higher levels of floral integration than those with generalists pollinators.6 Thus, the Darwinian view of flowers as highly specialized mechanic devices (and therefore highly integrated structures) has become the paradigm among floral biologists.7, 8 However, after more than a century of Darwin’s ideas, there is a lack of empirical evidence of the adaptive value of the extent of floral integration. Thus, we are still far from rejecting/accepting this hypothesis given the absence of studies on the adaptive value of floral integration. Although the comparative method has provided some insights about the importance of phenotypic integration with respect to historical contingencies,5, 9 we still do not know if natural selection promotes flower integration. On the other hand, Lande and Arnold10 have encouraged the study of natural selection with a multivariate approach, but few empirical studies have shown consistent evidence that selection favors the coordinated expression of floral attributes (e.g., significant correlational selection gradients).11 Moreover, we still do not know the magnitude of the natural levels of floral integration that characterize flowering plants, and so we are unable to make contrasts with the few existing empirical studies and to determine the magnitude of integration that we should consider high or low (Fig. 1A, B and D). Thus, in order to determine the adaptive value of floral integration we used three complementary approaches. In four species of Rosaceae (two populations each) we applied the comparative method, hierarchical selection analyses on floral integration, and performed a review of the available literature to assess the distribution of levels of floral integration among flowering plants.

Our results following the comparative method indicated that although species and clades showed significant differences in the variance-covariance structure of the flower, they present similar levels of floral integration (22.08%).12 Hierarchical selection analyses on individual floral traits, scores from principal components (intrafloral integration) and the integration of the whole flower indicated that...
natural selection acted on individual traits and on intrafloral integration, but not upon the integration of the whole flower (Fig. 1C). Additionally, our review indicated that the mean level of floral integration among flowering plants is 21% of the maximum possible integration. This value resulted lower than that expected by chance (33%), supporting the idea that plants have low levels of floral integration. Altogether, the three components of our study suggest a low adaptive value of floral integration.12

Why Plants have Low Levels of Floral Integration?

There are at least two possible answers to this question. First, evidence has accumulated during the last decades indicating that the selection pressures exerted by pollinators may fluctuate through time, thus precluding the evolution of high levels of floral integration. In addition, several other selective agents can act upon the floral phenotype such as herbivores, florivores, nectar robbers and parasites among others. It is common that different selective pressures act in opposite directions, potentially constraining the evolution of high levels of matching between the floral phenotype with the most important pollinator (i.e., a high level of floral integration) (Fig. 1A). Moreover, selection acting on fruit (dispersal) traits could also constrain the evolution of high levels of floral integration because of developmental linkage, limiting the evolution of high levels of floral integration.12 However, some of the most overwhelming examples of coadaptation between flowering plants and pollinators point out that the fusion of floral parts was a repeated evolutionary path followed by several lineages of plants increasing the extent of floral integration. In these cases, merging floral structures increased floral integration and is likely to represent an adaptation. Hence, besides the possible existence of constraints these cases suggest that such constraints have been overcome by different groups of species in several families.

Second, generalized low levels of floral integration could have been favored during evolutionary history, either because natural selection maintains low levels of integration on the whole variance-covariance structure of the flower, or has acted mainly to increase the integration of subsets of traits (intrafloral integration) (Fig. 1C). Given that we found no evidence of selection acting on the integration of the whole flower but instead promoted intrafloral integration, the low level of integration found in our review suggests that (whole) floral integration has little adaptive value. In a companion numerical simulation we additionally demonstrated that increasing intrafloral integration would indirectly augment whole flower integration, and that very low levels of intrafloral integration (30%) are sufficient to produce the observed levels of floral integration. Thus, low levels of floral integration may constitute a by-product of selection acting on intrafloral integration. This explanation suggests that relatively few floral traits mediate the interaction with pollinators, while the relationships among the rest of the floral traits may be the result of developmental/historical contingencies. If high levels of integration represent an evolutionary constraint, low levels may facilitate diversification (evolvability).

The study of phenotypic integration has become a central issue in evolutionary biology. Although both micro and macro evolutionary studies would provide important empirical evidence to improve our understanding of the evolution of floral integration, to date, there are probably more questions than answers to understand the adaptive value of floral integration. In this sense, our study made useful comments on the final version of the manuscript.

Figure 1. Schematic representation of the different forms of association among characters in a structural or functional module. Each polygon represents a group of traits that characterize the module (i.e., flower). Line thickness indicates the degree of correlation between pairs of traits within a hypothetical module. Numbers represent characters that are components of an hypothetical module. (A) Highly integrated modules are those that present high levels of correlation between traits. (B) Modules with low levels of integration are those with weak correlations between characters. (C) Intrafloral integration indicate that a subset of characters (8, 2, 3 and 4) within the module present higher levels of correlation among them than with the rest of the characters. (D) A non integrated module can be represented by non existent or very weak correlations between characters.

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