

NATURAL SELECTION IN PLANTS 151 YEARS AFTER *THE ORIGIN*: INTRODUCTION

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The goal of this special issue is to survey the current state of our knowledge of natural selection in plants. Do we need yet another compilation inspired by the sesquicentennial of *The Origin* (Darwin 1859)? I believe we do, because to my knowledge no other Darwin-year collection has focused on natural selection in plants, and plants were crucially important to Darwin's development of the theory of natural selection (six of his books were on plants). Plants are still crucially important to the study of natural selection in the field (where all selection occurs) because their sessile nature means that individuals can be followed either in their natural locations or after transplantation to new habitats. Plants are also very well suited to experimental evolution because it is a simple matter to store past generations as seeds. This storage ability also means that plants could be used to make detailed studies of present-day rapid evolution, especially in response to anthropogenic environmental changes, if seeds from natural populations are systematically collected and stored now for future studies (Franks et al. 2008).

We conduct our survey of natural selection in plants through a mix of empirical reviews, conceptual reviews, and original research by established leaders in the field as well as younger investigators. We have papers addressing natural selection using both phenotypic and molecular approaches. Latta opens the issue with an overview of the central and closely related concepts of selection, adaptation, and variation. It is useful to begin this way for anyone not already very well-versed in these areas, as the literature is unfortunately rife with misunderstandings. Apparently, natural selection is difficult to understand deeply, despite its inherent simplicity.

While the contributors were picked solely to represent excellence across a broad spectrum and were encouraged to write about whatever topics they were most interested in, some themes emerged:

Selection on floral traits. The proportion of papers addressing selection on floral traits in the issue (Caruso et al., Ellis and Johnson, Gómez and Perfectti, Horvitz et al., Sletvold and Ågren) is surely higher than the overall importance of flowers to plant adaptation. This overemphasis on flowers is not just due to my personal bias, because studies of flowers are overrepresented among all studies of natural selection in plants. This may reflect human affinity with beauty (perhaps the only good explanation why we have two articles addressing selection on spur lengths in orchids), but I think more important is the relative ease of identifying and measur-

ing the key traits and studying their functional interactions with the main selective agents (pollinators). These tasks are more difficult for other plant traits such as physiology and vegetative morphology. However, given their importance to adaptation and survival in sessile organisms, more studies of selection on these latter traits are needed; for an example, see the contribution by Mazer et al.

Nonpollinator sources of selection on floral traits. Most studies of floral evolution assume that pollinators are the only selective agent, but this assumption has been called into question by recent studies demonstrating non-pollinator-mediated selection on floral traits (e.g., Galen and Cuba 2001; Irwin et al. 2003). Two articles in the issue (Caruso et al., Sletvold and Ågren) use a relatively new technique to test this assumption and isolate pollinator-mediated selection. This is done by comparing selection on plants that are saturated with pollen experimentally, which represents selection by agents other than pollinators, to selection on naturally pollinated plants (often called "open pollinated"), which represents selection due to all selective agents, including pollinators. The difference between these two is inferred to be pollinator-mediated selection. Both articles found evidence for both pollinator- and non-pollinator-mediated selection on floral traits, although orchid spur length was under selection only by pollinators. The relative importance of pollinator-versus non-pollinator-mediated selection on floral traits is an entirely empirical question, and these articles add substantially to our meager knowledge in this area. In a related vein, Mazer et al. apply the non-pollinator-mediated selection idea to the evolution of mating systems, historically one of the most active areas of research in plant evolution. They provide evidence that selfing evolves as a consequence of selection for shortened life cycles in seasonally dry environments.

Spatial and temporal variation in selection. One of the more difficult challenges in understanding natural selection and adaptation in the wild is dealing with the high degree of spatial and temporal variation in selection. Both biotic and abiotic selective agents can vary widely within and among years and over short distances. Sletvold and Ågren report significant differences in selection across years and populations. Gómez and Perfectti show that spatial variation in selection on corolla shape matches patterns of preferences and abundances of the different taxa of pollinators and that these differences have resulted in local adaptation in corolla shape. This further suggests that the spatial variation is greater than the temporal variation within populations, as this is necessary for the evolution of local

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adaptation. Horvitz et al. present an analytical method to help empiricists deal with this ubiquitous variation in selection, enabling researchers to use longer-term data on environmental causes of selection (e.g., climate records) to extend short-term measurements of selection over longer periods.

Multiple selective agents. Multiple selective agents is a theme closely related to the previous three, as floral adaptation can be driven by multiple pollinators as well as by other biotic and abiotic selective agents (Caruso et al., Gómez and Perfectti, Mazer et al., Sletvold and Ågren), and the temporal and spatial variation in selection will often be due to multiple selective agents varying over time and space (Gómez and Perfectti, Horvitz et al.). Similarly, Sasu et al. show that squash plants with a virus-resistance transgene suffer less herbivore damage early in the season but more damage later in the season relative to nontransgenic controls. Surprisingly, this is only true in the presence of the virus; in the absence of the virus, the transgene has no significant effect on herbivore damage.

Constraints on adaptation. Despite the fact that constraints on adaptive evolution have been a major theme in the literature since Gould and Lewontin (1979), we really don't have a good understanding of the importance of constraints in evolution. Constraints have been most commonly studied using a quantitative genetic approach, and a number of different methods have been proposed to quantify genetic constraints. Simonsen and Stinchcombe apply all these methods to the same *Ipomoea* data set and get different quantitative predictions of constraint, both from different methods and depending on whether or how the traits are standardized. Thus, it seems clear that better methods for predicting constraints are needed, or at least a greater consensus on which methods are best and under what circumstances. Colautti and Barrett apply constraint theory to an invasive species (*Lythrum salicaria*). They find selection for earlier flowering at a larger size but that this evolution of these traits may be constrained by a genetic correlation between them.

Inferring selection from sequence data. The articles by Hohenlohe et al. and Charlesworth et al. clearly delineate both the promise and the pitfalls of using sequence data to infer selection. An exciting development is that we are now able to apply these techniques to nonmodel organisms. Our ability to infer selection from sequence data will improve rapidly as sequencing costs continue to plummet, making population samples of whole-genome sequence available in the near future. However, better analytical techniques will be necessary as well.

Conclusions

Are there overall conclusions we can draw about the study of natural selection in plants in the year 2010? First, it is still dominated by studies of phenotypic selection. This might be a bit disappointing in this era of stunning progress in molecular techniques, but since selection *is* a causal relationship between fitness and a phenotypic trait, a strong emphasis on the phenotype will always be crucial. Still, there are many

questions about natural selection and adaptation that continue to be difficult to answer because we don't know the molecular genetic underpinnings of the adaptive traits; examples include trade-offs and constraints (Agrawal et al. 2010).

Second, the absence of studies of selection through male fitness certainly is disappointing, at least to me, because the techniques for doing this have been available for decades now and are only getting easier. This is mainly done using molecular genetic paternity analysis, but it can also be done using labeled pollen, as shown by Ellis and Johnson. The Ellis and Johnson article also demonstrates that measures of pollen removal will often not be good proxies for male fitness (Harder and Thomson 1989; Conner et al. 2003). Bateman's principle, that selection on sexually selected traits should be stronger through male than through female fitness, may not always hold for floral traits, especially when female reproduction is limited more by pollinator service than by abiotic resources like light, water, and nitrogen (Wilson et al. 1994; Ashman et al. 2004). However, even when female fitness is limited by pollinators, much of selection on floral traits (as well as other traits) is likely to be through male fitness; the relative importance of male versus female fitness differences in driving floral adaptation will be an open question until more studies are performed that measure selection through both seed set and seed siring success.

Third, the study of selection through sequence analysis alone is still promising and is still fraught with difficulty, but perhaps with the ability to sequence whole genomes on reasonable samples of multiple populations, these difficulties will abate somewhat. What we really need is a true integration of phenotypic and molecular approaches, where we can understand adaptation in nature at the level of gene sequences. We still seem to be on the cusp of this, and there have been some notable recent successes with what are essentially Mendelian traits in animals (e.g., Hoekstra et al. 2006; Chan et al. 2010). Because QTL mapping was pioneered in plants (Paterson et al. 1988), as was the use of QTL mapping in natural populations (Bradshaw et al. 1995), it seems likely that studies of plants will be at the forefront of the merging of quantitative and population genetics. A reasonable goal for the near future is to be able to estimate single-locus or perhaps even single-nucleotide selection coefficients in nature and to identify the selective agents in the environment responsible for this selection. While the molecular tools, especially sequencing technology, are advancing very rapidly, understanding selective agents and measuring fitness in the field will continue to depend on long hours in the field and a thorough knowledge of the natural history of the organism. Natural selection occurs only in nature, and therefore it needs to be studied in nature.

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