



Phylogenetics and Its Role in Successful Plant Breeding System Evolution

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Dobzhansky stated that nothing in biology makes sense except in the light of evolution. Everything makes a lot more sense in the light of phylogeny. It is only recently that phylogenetic approaches have been used to address questions about the evolution of plant reproductive systems and plant-pollinator interactions. The development of cladistic approaches that define monophyletic groups on the basis of shared, derived character states, combined with the emergence of molecular systematics, has resulted in an explosion of phylogenetic studies and an increased awareness of the need for interdisciplinary approaches combining ecological and systematic methodology. Character mapping may be especially useful for detecting convergent evolution. The insights provided by character mapping are determined by a number of factors, including the degree of confidence in phylogenies underlying these studies and the identification of appropriate outgroups. Assumptions about character coding, character ordering, inclusion vs. exclusion of characters that are mapped on trees in the data matrix, and weighting of characters will have profound effects on interpretation of character evolution. Highly labile characters that evolve frequently and have the potential to undergo reversals may make it difficult to detect the pattern of character evolution. While not a simple cure to understanding problems that have been studied only in the realm of microevolutionary studies, phylogenetic approaches offer clear potential for providing new insights for evolutionary studies.

Introduction

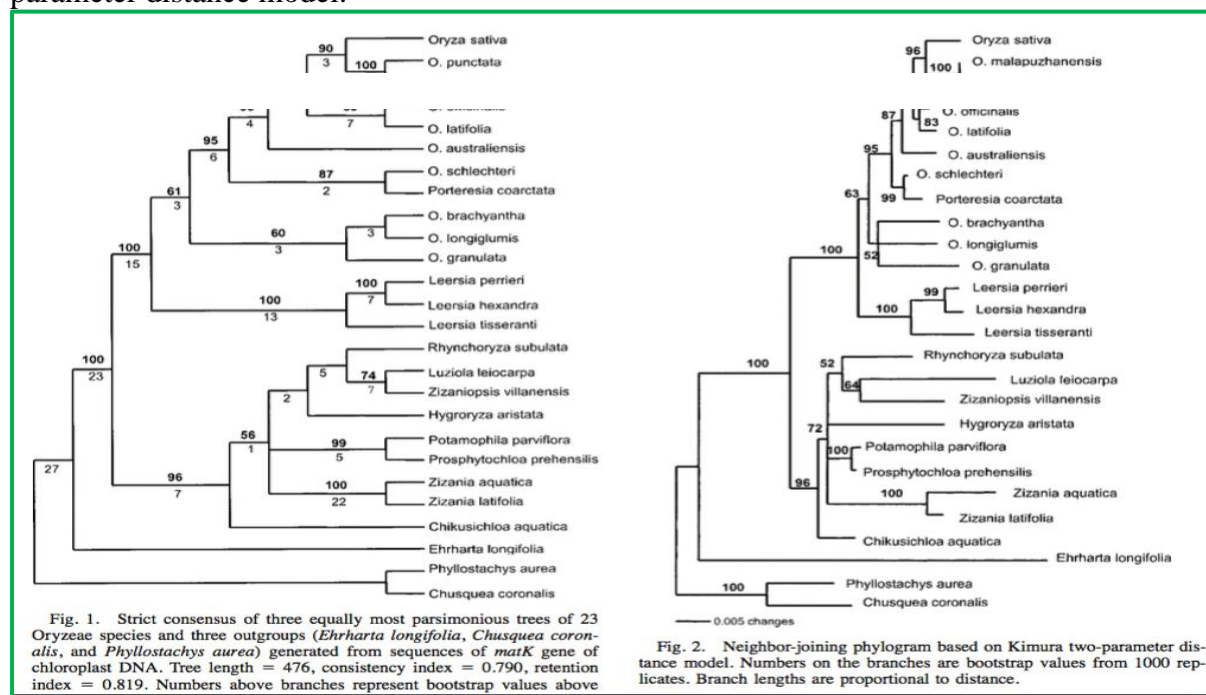
Phylogenetics is the study of the ancestral relatedness of groups of organisms, whether alive or extinct. The field of phylogenetics takes a functional and more scientific turn in its attempts to construct an objective depiction of evolutionary relationships between organisms based on genetic, molecular, archaeological, and historical studies and with the specific purpose of explaining, predicting, and testing similarities and differences between organisms. The evolutionary relatedness between species is reflected by branching pattern of the tree and the relative distance between species on the tree, also called the “tree of life”. These phylogenetic approaches offer the hope of understanding the historical context for the evolution of character evolution, including plant reproductive systems. The potential for understanding both the number of times a character state has evolved and the timing of the evolution of that character state relative to environmental shifts is a powerful complement to population-level studies, which provide detailed information but are necessarily limited to one or a few populations, often of a single species. The goal is to determine how these macroevolutionary approaches have extended our understanding of plant reproductive biology beyond the insights derived from studies of microevolutionary processes.

Need for Phylogenetic Approaches

Most systematists and evolutionary biologists agree that phylogenies should be the central underpinning of research in much of biology. For example, it is critical to place model organisms in the appropriate phylogenetic context to obtain a better understanding of both patterns and processes of evolution. Dobzhansky stated that nothing in biology makes sense except in the light of evolution. A close corollary is that everything makes a lot more sense in the light of phylogeny. For example, the fact that tomato, *Lycopersicon esculentum*, is actually embedded within a well-marked clade of *Solanum* species and is therefore really a species of *Solanum* rather than a distinct genus, is a powerful evolutionary statement. This discovery is of great importance to plant breeders, in that it reveals the closest relatives of *Lycopersicon esculentum* (now known as *Solanum lycopersicon*) and points to these relatives as the focal points for detailed future studies.

Phylogenetic tree reconstruction

A phylogeny is a tree containing nodes that are connected by branches. Each branch represents the persistence of a genetic lineage through time, and each node represents the birth of a new lineage. If the tree represents the relationship among a group of species, then the nodes represent speciation events. In other contexts, the interpretation might be different. Fig 1 and Fig 2 shows the phylogenetic tree of oryzae species generated from sequences of matK gene of chloroplast DNA and neighbor joining phylogram based on Kimura two parameter distance model.



Phylogenetic trees are not directly observed and are instead inferred from sequence or other data. Phylogeny reconstruction methods are either distance-based or character-based. In distance matrix methods, the distance between every pair of sequences is calculated, and the resulting distance matrix is used for tree reconstruction. Character-based methods include maximum parsimony, maximum likelihood and Bayesian inference methods. These approaches simultaneously compare all sequences in the alignment, considering one character (a site in the alignment) at a time to calculate a score for each tree.

Identification of Appropriate Outgroups

Correct identification of the outgroup, the taxon most closely related to the group under study, is critical for identification of ancestral character states within lineages and is therefore of fundamental importance to character mapping (Donoghue *et al.*, 1984; Maddison *et al.*, 1984). When outgroups cannot be identified with certainty, the outgroup substitution approach may be a satisfactory alternative (Donoghue *et al.*, 1984). Using this approach, the ancestral state of the character is determined using a variety of potential outgroups, and the effects of varying the outgroup on character mapping are analyzed. The current widespread self-incompatibility in the silverswords (Carr *et al.*, 1986) is therefore likely to be the result of colonization by a self-incompatible ancestor of this lineage. Unfortunately, precise outgroup identification is often problematic.

Character Inclusion or Exclusion

Whether characters that will be mapped on trees should be included in the morphological data matrices used to produce trees has been debated extensively. A commonly held view is that inclusion of these characters is circular because taxa possessing a character state would group together and cases of multiple evolution of the character state (homoplasy) would be missed (Armbruster WS., 1992; Brooks *et al.*, 1991; Silvertown *et al.*, 1996). In contrast, others (Swofford *et al.*, 1992) argue that traits should be included if they are phylogenetically informative. Even with substantial homoplasy, these characters may be useful in phylogenetic reconstruction, assuming that there are enough unrelated characters that homoplasy can be detected. Phylogenetic analysis was used to determine whether bat pollination in *Parkia* (Fabaceae) has evolved on separate occasions in the New and Old World (Luckow *et al.*, 1995).

Character Coding, Ordering, and Weighting

How characters are coded and whether characters are ordered may have profound effects on interpretation of character evolution. The effects of differences in character coding can be seen in *Schiedea*, where coding the breeding system as four states (hermaphroditic, gynodioecious, subdioecious, and dioecious) rather than two states (hermaphroditic, dimorphic) resulted in a greater number of hypothesized transitions from hermaphroditism to dimorphism (Weller *et al.*, 1995).

Ordering of character states and binary character coding have similar effects on the estimation of numbers of transitions to derived character states. In *Schiedea*, ordering of characters resulted in fewer transitions to gynodioecy and more reversals to hermaphroditism. Character weighting, where transitions between character states are more likely in one direction than the other, will have major effects on interpretation of character evolution. Using morphological phylogenetic data, Graham *et al.*, 1993 concluded that tristylly in the Lythraceae has evolved on at least five occasions. A weighting scheme that favored loss of heterostyly over gains would presumably have resulted in substantial modifications of the phylogeny, especially in view of the limited number of characters used for the analysis, and fewer transitions to heterostyly.

The examples illustrate the complexity of issues related to character delineation and assumptions about these characters. Although the use of phylogenetic trees for the analysis of character evolution may appear to be an objective means of obtaining additional insights into evolutionary processes, it seems clear that in many cases, prior views of character evolution may strongly influence results.

Phylogenetic Approaches for Analysis of Character Evolution

Clearly, phylogenetic approaches may be most useful in lineages with well-supported phylogenies including a large proportion of extant species. Character mapping in lineages in

which there has been considerable extinction (or where there are regions of the phylogeny with less branching) may be difficult if extinct sister taxa had different character states than did extant species. Using phylogenies to determine the order of evolutionary events (and thus provide inferences of causality) is likely to work best when cause and effect are not very strongly related. The evolution of complex character traits is more likely to be interpreted correctly using phylogenetic analysis, particularly when homoplasy can be reinterpreted as cases of independent gains of superficially similar character states. It seems more likely, however, that phylogenetic approaches will continue to have a critical role in identifying cases where true homology is more restricted than cursory examination might suggest. While not a simple cure to understanding problems that in the past have been studied only in the realm of microevolutionary studies, phylogenetic approaches offer clear potential for providing new insights.

Summary and Future Prospects

An exciting recent development is the merging of phylogenetics and genomics. Phylogenetic hypotheses have become the framework for the choice of organisms in genomic analyses, and more and more molecular biologists are using phylogenetic trees to guide their sampling of taxa for comparative research. This trend will continue. Systematics is moving rapidly; therefore, molecular biologists are encouraged to contact systematics “experts” for help in obtaining the best supported trees for a given clade of interest. We stress the importance of a rigorous phylogenetic analysis of data. A thorough phylogenetic analysis, evaluating alternative alignments, exon versus intron boundaries, using different phylogenetic methods, and obtaining estimates of internal support, may take several weeks or more, and this should not be considered an unreasonable investment of time.

Conclusion

Phylogenetic trees provide a critical underpinning, not only for systematic studies, but also for investigations of molecular evolution and comparative genetics. Considerable progress in reconstructing phylogeny has been made at all levels in the green plant hierarchy of life, particularly among the angiosperms. Phylogenetic hypotheses present excellent opportunities for broadly based investigations of molecular evolution, including studies of the diversification of gene families. In addition, a number of so-called model organisms as well as a number of crops have now been placed in the appropriate phylogenetic context; sister taxa and a clade of closest relatives have been identified. Phylogenetic hypotheses provide the opportunity to extend the knowledge garnered from the study of such model organisms to the closest relatives of this plants in natural population.

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