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Speciation in flowering plants: an overview

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Abstract: The great biological diversity prevailing on the planet earth is the result of speciation taking place since life originated over 3.5 billion years ago. Speciation is the result of natural selection acting on heritable variations. The common definition of species, generally practiced by taxonomists, is a group of individuals that is morphologically distinct from other groups. The literature on speciation is extensive and most of the reviews cover one or another aspect of speciation rather than the entire field. In this review, an attempt is made to provide an overview on speciation, particularly the definitions, requirements, various modes and pathways including an outlook proposed on the rate of speciation in the coming decades due to ongoing human-induced environmental and biological changes, keeping in view the non-specialists.

Key words: Allopatric mode, Floral traits, Hybridization, Pollinator-driven speciation, Polyploidy, Sympatric mode.

Introduction

The planet Earth holds an enormous biological diversity made up of plants, animals, and other eukaryotes and prokaryotes. Until Darwin proposed his theory of evolution, all life forms present on the planet were believed to be created by God and they were thought to be immutable over the course of time. Following the publication of Darwin's theory of evolution (Darwin, 1859), the creationist concept was gradually replaced by an evolutionary concept which explained the origin of new species as a result of natural selection acting on heritable variations. Over the years, evolution has become one of the most important concepts in biology. According to the noted geneticist, Theodosius Dobzhansky (1937) 'Nothing in biology makes sense except in the light of evolution'. The static species concept of Linnaeus has now been replaced by a dynamic species concept and the population has become the unit of speciation (see Stebbins, 1950; Hey *et al.,* 2005; Lexer & Widmer, 2008). Thus, the biological diversity currently prevailing on Earth is the result of evolutionary processes operating since life originated over 3.5 billion years ago (Lazcano & Miller, 1996; Patel *et al*., 2015). The best working estimate of the number of eukaryotic species present on the planet ranges from 8.7 million to 12 million, of which only about 1.2 million have so far been scientifically documented (see Mora *et al*., 2011; Raven, 2020). Rapid diversification of angiosperms has been the subject of continuous debate for more than 100 years (see Crane *et al.,* 2000; Crepet & Niklas, 2009; Magallón & Castillo, 2009; Smith *et al*., 2011; Bao *et al.,* 2019). Based on fossil evidence, the origin of angiosperms was traditionally considered to be in the Cretaceous period ranging from 110 to 135 million years ago. However, in recent years, based on molecular data, the origin of angiosperms has been pushed back to the late Triassic period about 210 million years ago (see Coiro *et al.,* 2019, Li *et al*., 2019, Janssens *et al*., 2020, van der Kooi & Ollerton, 2020).

There is no definition of species that is universally accepted or valid under all circumstances (Mayr, 1942; Simpson, 1951; Queiroz, 2007). The morphological species concept, practiced by most taxonomists, defines species as a group of individuals that is morphologically distinct from other groups.

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According to the biological species concept (Mayr, 1942) a species is made up of 'groups of naturally or potentially interbreeding individuals which are reproductively isolated from other such groups'. Thus, morphological dissimilarity and reproductive isolation are the two major criteria for distinguishing species. The biological species concept, however, is difficult to apply as a routine concept since there are practical difficulties to investigate reproductive isolation of a potential new species with related species. Further, reproductive isolation is not absolute in many of the plant species; some hybrids do form between well-defined related species, although most of them may not establish as new species. Also, a number of molecular studies have shown gene flow is quite common between populations and species. In fact, as discussed later, speciation through hybridization is considered as one of the major pathways as far as plants are concerned. Thus, the biological species concept has limitations for routine use in plants, although it is prevalent in animals (Grant, 1981). Generally, taxonomists who erect new species continue to use a morphological definition of species.

There are two other species concepts that are not very prevalent in the literature. According to the phylogenetic species concept 'the smallest diagnosable cluster of individual organisms within which there is a parental pattern of ancestry and descent' (Eldredge & Cracraft, 1980) is considered a species. It tries to define species by their relationships to other species based on their genealogical relationships. A group of individuals that includes all the descendants of one common ancestor is referred to as a monophyletic group. According to Wiley's (1978) evolutionary species concept, a species is a lineage of interbreeding organisms, reproductively isolated from other lineages, that has a beginning (*i.e.*, speciation through reproductive isolation from the parent population), an end (*i.e.*, either with extinction or with its branching into one or more descendants), and a distinct evolutionary trajectory.

Speciation is a prolonged and complex process and can take hundreds or thousands of generations. Unlike many other biological events, most of the evidence related to speciation is indirect and cannot be easily replicated or demonstrated. A general understanding of speciation is largely based on field observations and analysis. Speciation has been discussed extensively since the 1930s by a number of investigators and a vast literature has accumulated on the subject (*e.g.*, Dobzhansky, 1937; Mayr, 1942; Stebbins, 1950; Grant, 1981; Fenster *et al.*, 2004; Hey *et al.*, 2005; Rundle & Nosil, 2005; Rieseberg & Willis, 2007; Abbott *et al.*, 2008; Cozzolino & Scopece, 2008; Lexer & Widmer, 2008; Kay & Sargent, 2009; Soltis & Soltis, 2009; Ferrer & Good, 2012; Yuan *et al.*, 2013; Levin, 2019). Most of the reviews are confined to comprehensive discussion covering one specific aspect of speciation, such as modes of speciation (Butlin *et al.,* 2008), pollinator-driven speciation (Hoballah *et al.,* 2007; Kay & Sargent 2009; Xu *et al.,* 2012a,b; van der Niet *et al.,* 2014), reproductive isolation in general (Lexer & Widmer, 2008) or in relation to floral specialization (Ambruster & Muchhala, 2009), ecological adaptation (Rundle & Nosil, 2005; Sobel *et al.,* 2010), polyploidy (Wood *et al.,* 2009; Laport & Ng, 2017; Pelé *et al.,* 2018), hybridization (Ferguson & Sang, 2001; Gross & Riesenberg, 2005; Mallet, 2007; Rieseberg & Willis, 2007; Soltis & Soltis, 2009; Alix *et al.*, 2017) and also speciation in the coming decades due to ongoing human-induced environmental changes (see Thomas, 2015; Levin, 2019). Hardly any review covers the whole concept of speciation. Although speciation is basic to all branches of biology, not all botanists, particularly in structural and functional disciplines, are familiar with basic concepts of speciation. An attempt is made here to give an overview of speciation in angiosperms, the most successful and highly diverse group amongst land plants without going too deep into all the complexities. This overview is essentially aimed to non-specialists and the references cited provide links to more comprehensive accounts on different aspects of speciation. Some terminologies associated with speciation are explained in Appendix 1.

Major requirements for speciation

Heritable variations, natural selection and reproductive isolation are the basic requirements for speciation. Presence of heritable variations is the primary requirement (Hoffman & Merilä, 1999). Mutations are the source of heritable variations and thus are the raw materials for speciation. Recombination during meiosis brings about additional variations by reshuffling of the mutated genes. Chromosomal and epigenetic changes, particularly under ecological stresses, also induce variations (Tsaftaris & Polidoros, 2000).

Natural selection acts on heritable variation and is the main operating force for speciation. Natural selection operates on mutations in three ways: if the mutation improves the fitness of the individuals under the prevailing environment, such mutants produce more progeny when compared to those without the mutated allele and gradually the individuals of the original population would get replaced with the mutants. If the mutation affects the fitness negatively, such individuals are less efficient in producing the progeny and they eventually get eliminated. If the mutation has no immediate effect on the fitness of the progeny, they are retained in the population until they affect the fitness positively or negatively. The action of natural selection is stronger when there is a change in the habitat; this generally happens when the individuals get dispersed to a new habitat (Rundle & Nosil, 2005; Sobel *et al.*, 2010).

Reproductive isolation primarily depends on some mechanism that prevents gene flow (movement of genes through space) between individuals within a population or between populations. As far as flowering plants are concerned, gene flow is brought about by dispersal of pollen, seeds and vegetative propagules. Reproductive isolation through the prevention of pollen-mediated gene flow is the most important mechanism for the initiation of speciation (Rieseberg & Willis, 2007). Pollination is the basis of pollen-mediated gene flow involving sexual reproduction. Details of reproductive isolation that operate between populations/species at different stages of sexual reproduction are presented in Table 1.

Modes of speciation

Allopatric speciation: Evolution of new species in geographically isolated populations as a result of intervention of some physical barrier, such as a rising mountain range or an expanding desert or river that prevents the movement of pollinators between the two populations. Allopatric speciation may also result without the development of new geographic barriers when individuals of a species

Table 1. Various steps in sexual reproduction at which reproductive isolation between populations/ species operate*.

Pre-pollination barriers Spatial or temporal isolation: The populations/species flower at different times or separated by geographical barriers/ distance so that the pollinators do not carry pollen across the barrier/distance. Change in pollinators' preferences as a result of changes in floral traits.
Post-pollination but pre-fertilization barriers Pollen grains that land on the stigma are inhibited from germination or pollen tubes from germinated pollen are inhibited in the pistil before reaching the ovule.
Post-fertilization barriers Degeneration of hybrid embryo at different stages of development. Even when hybrid embryos are formed, they may not germinate or hybrid plants may not flower or they may be sterile or the few hybrids formed are eliminated because of their poor fitness.

* Reproductive isolation due to pre-pollination barriers is the initial requirement; it is reinforced over time by pre- and post-fertilization barriers as a result of additional mutations, recombination, chromosomal and epigenetic changes.

colonize a remote area and thus its descendants become geographically isolated from the beginning because of the distance. Physical isolation prevents gene flow between the parental and isolated populations as the pollinators do not move across the barrier or distance. Thus, geographically isolated populations behave as local breeding units; any genotypic or phenotypic changes in them would not enter the original population.

Reproductive isolation initiated through pre-pollination barriers are gradually reinforced through the development of pre- and post-fertilization barriers over a period of time and the isolated population eventually evolves into a new species. Even if the two species subsequently come into secondary contact, they do not form fertile offspring due to genetic incompatibilities, or do not hybridize at all due to the prevalence of pre- and post-fertilization barriers (see Rundle & Nosil, 2005). Allopatric speciation is faster when isolated populations occupy different environments. Ecological differences may operate in the form of climate, niches, available resources or the presence of predators and competitors (Schluter, 2000). Thus, the newly established populations are subjected to stronger selective pressures and undergo genotypic and phenotypic divergence faster as they adapt to different environmental conditions. Allopatric speciation is considered to be the more common method of speciation when compared to sympatric speciation (Butlin *et al.,* 2008).

Sympatric speciation: This refers to the evolution of a new species within a population through the emergence of reproductive isolation between individuals of the original population. There are two major modes of sympatric speciation – pollinator-driven speciation and through polyploidization (see below).

Two other modes of speciation, peripatric (involving divergence of smaller peripheral populations) and parapatric (involving adjoining populations) are included in many books and earlier reviews (Coyne & Orr, 2004; Lawson *et al.*, 2015). These are now considered as a continuum between sympatric and allopatric speciation (Butlin *et al.,* 2008).

Pollinator-driven speciation

There is a general agreement amongst evolutionary biologists that insect pollination was the cause of rapid diversification of angiosperms recorded in the Cretaceous period (Magallón & Castillo, 2009; Smith *et al.,* 2011; Bao *et al.,* 2019). Many floral traits such as flower size and shape, their colour, display, and the quality and quantity of the rewards act as attractants for pollinators. A change in any of these critical floral traits of one or a few individuals within a population may attract a new pollinator instead of the original pollinator thus initiate reproductive isolation. Until recently some evolutionary biologists even doubted the possibility of pollinator-driven sympatric mode of speciation. This was because of the prevalence of the classical view that adaptive mutations generally have very small phenotypic effects and they may not be able to induce reproductive isolation. However, a number of recent studies have shown that a single major mutation may initiate adaptive shift in pollinator preferences (Hoballah *et al.*, 2007; Xu *et al.,* 2012b; Yuan *et al.,* 2013; Fattorini & Glover, 2020). Thus, species isolation may be achieved by mutation of even just one or a modest number of genes. Pollinator-driven speciation can operate in species which show some degree of floral specialization in attracting a single species of pollinator or one functional group of pollinators such as bees or humming birds or bats, and not easily in generalized pollination systems in which diverse groups of pollinators are effective in transferring pollen (see Fenster *et al.*, 2004; Armbruster & Muchhala, 2009; Kay & Sargent, 2009).

Detailed studies in species of *Mimulus* and *Petunia* have provided strong evidences for pollinator-driven speciation by documenting specific genes that induce new floral phenotypes leading to a change in pollinator preference (see Yuan *et al.*, 2013). Of these, *Mimulus* is one of the well-investigated systems (Bradshaw *et al.*, 1995; Schemske & Bradshaw, 1999; Bradshaw &

Schemske, 2003). *Mimulus* has about 120 species showing great variation in floral phenotypes, pollinators and breeding systems. For example, *Mimulus lewisii* grows only at moderate and higher elevations (1600–3000 m), has pink flowers and small amount of nectar, and bumblebees are the pollinators. Its sister species, *M. cardinalis* grows at lower to high elevations (sea level to 3000 m), has red flowers and larger amount of nectar, and humming birds are the pollinators. Although their ranges overlaps at high and moderate elevations in the mountains of California, hybrids are exceedingly rare. The petal colour in these two sister *Mimulus* species is determined by carotenoid pigments controlled by one quantitative locus, *YELLOW UPPER (YUP)*. The dominant *YUP* allele in *M. lewisii* prevents carotenoid deposition and the flowers are pink that attracts predominantly bees (Bradshaw & Schemske, 2003). The recessive *yup* allele in *M. cardinalis* promotes carotenoid deposition in the petals and the flowers are red. The red flowers do not attract bees effectively but they mostly attract humming birds.

An interesting experiment confirmed the role of petal colour in attracting bees or hummingbirds in these two *Mimulus* species (Bradshaw & Schemske, 2003). Near isogenic lines *M. cardinalis* carrying the dominant *YUP* allele from *M. lewisii* produced pink flowers. The bees showed strong preference for pink flowers of *M. cardinalis* over red flowered wild type. On the other hand, near isogenic lines of *M. lewisii* carrying recessive *yup* allele from *M. cardinalis* produced yellowish-orange flowers; hummingbirds showed strong preference for these flowers. It was the colour of the corolla that changed the pollinator visits and not the shape of the corolla or the amount of nectar in the isogenic lines. Thus, a single trait variation in the flower colour, controlled by one quantitative locus, was enough to initiate a change in pollinator preference and thus to potentially initiate reproductive isolation.

Another example comes from *Petunia*. *Petunia integrifolia* has purple scentless flowers with limited nectar and bees are the pollinators whereas *P. axillaris* has white fragrant flowers with considerable amount of nectar and hawkmoths are the pollinators (Hopkins & Rausher, 2012). The colour difference between *P. integrifolia* and *P. axillaris* was shown to be determined by one gene *ANTHOCYANIN2 (AN2)* (Quattrocchio *et al*., 1999; Hoballah *et al*., 2007) that is involved in anthocyanin biosynthesis. Loss of *AN2* function results in white flowers, as is the case in the wild type *P. axillaries*. Transformation of the functional *P. integrifolia AN2* allele into *P. axillaris* background resulted in purple flowers; all other floral characters remained that of the original *P. axillaris* (Hoballah *et al*., 2007). Interestingly, bumblebees showed a preference for the transformed purple flowers of *P. axillaris* while hawkmoths continued to show a preference to wild type white flowers over purple flowers. Thus one mutation changing the colour of the petal of *P. axillaris* shifted pollinator preference of moths to bees. Subsequent mutations of other traits such as the amount of nectar and scent could stabilized pollinator preferences.

The examples of *Mimulus* and *Petunia* described above show pollinator discrimination of the flowers based on visual traits that are controlled by a single gene in each species. There are several other examples of single gene controlled floral traits (Hopkins & Rausher, 2012; Clegg & Durbin, 2000; Byers *et al*., 2014) indicating the role of even a single mutations in initiating reproductive isolation through a change in pollinator preferences in sympatric populations.

Highly specialized species-specific pollination systems: In a number of species the pollination system is highly specialized in which each plant species is pollinated by just one specific animal species. Although there are quite a few cases of highly specialized pollination systems reported (see Johnson & Steiner, 2000; Pellmyr, 2002; Galliot *et al*., 2006; Willmer, 2011; Shivanna, 2014; Kato & Kawakita, 2017), only two such systems, nursery pollination (figs and fig-wasps) and sexual deception (orchids), are described here in relation to speciation.

Nursery pollination in figs: There are about 850 species of *Ficus* and based on our present knowledge, each species of *Ficus* is considered to be pollinated by a species–specific female fig-wasp species (Wiebes, 1979; Pellmyr, 2002; Weiblen, 2004; Willmer, 2011). Floral scent is a key factor in attracting these species-specific pollinators. The composition of floral scent of each *Ficus* species reflects species boundaries (Chen *et al*., 2009; Proffit *et al*., 2008; Wang *et al*., 2013). For example, *Ficus semicordata* is pollinated by the fig-wasp, *Ceratosolen gravelyi*. One benzenoid compound, 4-methylanisole, is the predominant component (94–98%) among the volatile compounds emitted by the receptive fig inflorescences (when they are at the female phase). This compound is entirely absent in the volatiles emitted by fig, four days after pollination, when they no longer attract pollinators. This compound is also absent in the volatiles emitted by two other sympatric fig species, *Ficus racemosa* and *Ficus hispida*, both of which are pollinated by other fig-wasp species. Even in laboratory experiments, 4-methylanisole attracts the species-specific pollinator, *C. gravelyi*. Chemical blends of volatiles lacking this compound do not attract this pollinator. Volatile compounds emitted by receptive figs of the two other sympatric fig species (*Ficus racemosa* and *Ficus hispida*) also do not attract the pollinator of *F. semicordata* (Whitehead & Peakall, 2009).

Sexual deception in orchids: A large number of orchids achieve pollination by sexual deception/mimicry. Their flowers do not offer any rewards but mimic virgin females of the pollinator and also emit a fragrance similar to sex pheromones of virgin females of the pollinator. The male visitor is attracted to the flowers based on olfactory and visual cues, and lands on the flowers. It tries to copulate (termed pseudo-copulation) and brings about pollination during this process by transferring pollinia gathered by previous visits to other flowers (Ayasse *et al*., 2003; Schiestl *et al*., 2003; Galizia *et al*., 2005; Renner, 2006; Xu *et al.,* 2011). Species of *Ophrys* are well-studied examples on sexual deception. Although several *Ophrys* species grow sympatrically, each species emits a different fragrance and is pollinated by different species of pollinator. For instance three species of *Ophrys*, *O. lupercalis, O. bilunilata,* and *O. fabrella*, use the same odour compounds for pollinator attraction, but in different proportions (Stökl *et al*., 2009). This changes the fragrance of each species. Thus, a change of floral odour brought about by the amounts of its components can result in the attraction of a different pollinator in these *Ophrys* species.

In some deceptive orchids, it has been experimentally shown that male pollinators are attracted even to plastic beads spiked with pheromone attractants and attempt to copulate with them (Peakall *et al*., 2010; Bohman *et al*., 2014). Thus, chemical signals alone can mediate attraction of species-specific pollinators. The shape of the flower does not seem to be so important in attracting pollinators; the correct position of the reproductive structures, however, plays a role in effective cross-pollination. Evidence collected so far indicate that changes in floral odour in sexually deceptive orchids are controlled by few genes with large phenotypic effects (see Schiestl *et al.,* 2003; Xu *et al*., 2012a,b). A mutation that results in a change in the floral odour is enough to attract a new pollinator that is not attracted by the parental species. This prevents pollen flow to the mutant with changed scent from other individuals of the population. The progeny from the mutant gradually evolves into a new species by reinforcement of other genotypic and phenotypic changes over time.

In fact speciation in sexually deceptive orchids is often based on its pollinator; the populations that do not share the same pollinator have been often considered as different species, independent of their morphological or genetic differences (Stökl *et al*., 2009; Peakall *et al*., 2010; Xu *et al*., 2012a,b). Reproductive isolation in closely related sexually deceptive orchids is largely due to pre-pollination barriers, *i.e.* differences in pollinator attraction; pre- and post-fertilization barriers tend to be weak or even absent. For example sympatric closely related species of *Ophrys*, *O. exaltata, O. garganica* and *O. sphegodes* attract species-specific solitary bees and do not share their pollinators. However, interspecific hand pollination results in fertile seeds but also fertile hybrids (Xu *et al.*, 2011).

Sustenance of specialized pollination systems during speciation: Plant species with highly specialized species-specific pollination syndromes have many advantages (Pellmyr, 2002; Willmer, 2011; Phillips *et al.*, 2017; Shivanna, 2019). The main advantage being that it increases pollination efficiency as it minimizes pollen loss by preventing pollen wastage to stigmas of other species and also stigma plugging by heterospecific pollen. However, super-specialization also carries many disadvantages. The spread of plant species to new locations is dependent on the availability of their species-specific pollinator, which may often be a major limitation. There is a possibility of pollinators abandoning plant populations when their density goes down below a limit. In nursery pollination systems, both the plant species and their pollinators are dependent on each other for sexual reproduction also; when one of the partners becomes scarce or extinct, the other partner is also prone to eventual extinction. Because of these disadvantages, several investigators since the time of Cope (1896) considered super-specialized pollination systems as 'evolutionary dead ends' prone for extinction (Tripp & Manos, 2008; Rentsch & Leebens-Mack, 2014).

The prevailing concept on speciation in highly specialized pollination systems has been that it is the result of co-evolution of the flower and the pollinator. Both the plant species and the pollinator species have undergone simultaneous diversification through joint co-speciation and adaptive radiation (Sanderson & Donoghue, 1996; Schluter, 2000; Good-Avila *et al.*, 2006); when the plant species splits into two daughter species, its mutualistic pollinator also splits. Several investigations in recent years are not entirely in agreement with this concept of co-speciation of the plant and the pollinator (Molbo *et al.*, 2003; Cruaud *et al.,* 2011; Vereecken *et al.*, 2012; Shivanna, 2019). It is difficult to expect simultaneous co-speciation of the pollinator that responds to the new odour of the plant species that has diversified from the parent species. It may take many generations of new plant species before its new pollinator evolves and the new mutualism establishes. How would they survive until a new pollinator evolves and establishes?

Highly specialized pollination systems have evolved several flexible strategies, to survive under pollinator constraints (see Shivanna, 2019).

i) Opting out of obligate mutualism by recruiting additional pollinators. A number of studies, mentioned below, have reported that many super-specialized pollination systems are capable of undergoing reversals from specialized to generalized modes. Cruaud *et al.* (2011) reported one wasp species pollinating at least 50 species of figs and wasp species which are genetically indistinguishable pollinating different host species (see also Molbo *et al.*, 2003; Machado *et al.*, 2005). Similarly in orchids also, there are several reports of gene flow and hybridization amongst sympatric, sexually deceptive species (Danesch *et al.*, 1975; Stökl *et al.*, 2009; Schiestl & Ayasse, 2002; Schiestl *et al.*, 2003; Cozzolino *et al.*, 2005; Cozzolino & Scopece, 2008; Gogler *et al.*, 2009).

ii) Evolving an autogamous (self) pollination mode (Catling, 1990; Bond, 1994; Neiland & Wilcock, 1994, 1995; Johnson & Steiner, 2000; Peter & Johnson, 2009). This is highly prevalent in orchids; about 30% of orchid species investigated are reported to be autogamous (Neiland & Wilcock, 1994, 1995; Claessens & Kleynen, 2002).

iii) Rely on or shift to vegetative propagules (*e.g.* Wang *et al.,* 2004). Further, obligate pollination systems are largely confined to perennials and/or those with the capacity for vegetative propagation (Shivanna, 2019). These adaptations enable them to survive for a number of years/generations until the evolution of new plant - pollinator and eventual stabilization of a new obligate pollination systems.

Polyploidy

Whole genome duplication, *i.e.* autopolyploidy, is common in plants, particularly in vascular plants, when compared to animals, and is an important driver of diversification (Jones, 1970; Stebbins, 1980; Bodt *et al.,* 2005; Wood *et al*., 2009; Levin, 2002, 2019; Ren *et al*., 2018; Clark & Donoghue, 2017; Landis *et al.,* 2018; Cui *et al.,* 2019; Gao, 2019; Qiao *et al.,* 2019; Zhang *et al*., 2019; Lavania, 2020). The most common pathway of autopolyploid production in the population is through the fusion of unreduced gametes; environmental stresses increase the production of unreduced gametes (see Levin, 2019). Extensive genome-wide studies on genomics in recent years have indicated that all angiosperms have undergone at least one event of polyploidization in their evolutionary history (*e.g.* Levin, 2002; Jiao *et al*., 2011; Soltis *et al*., 2014; Landis *et al*., 2018; Ren *et al.,* 2018; Qiao *et al.,* 2019). Although a proportion of duplicated genes are retained for long periods, often the genome is reduced in size due to differential loss of genes (genome downsizing) and the chromosome numbers are reduced due to their loss or fusion over time (Leitch & Bennett, 2004; Storme & Mason, 2014). Loss of chromosomes in polyploid lines indicates that some of the species even with low chromosome numbers may have derived from polyploid ancestry (see Wood *et al*., 2009). Polyploidization has contributed to the evolution of novel functions including resistance to diseases and other stresses (see Panchy *et al*., 2016 and references therein). Polyploids, of both auto- and allopolyploid origins (see below), may disrupt both genetic and epigenomic processes resulting in altered DNA methylation patterns, changes in gene expression and reactivation of transposable elements (Levin, 2002; Alix *et al*., 2017; Edger *et al*., 2017; Pelé *et al*., 2018). Several investigations have shown the role of epigenetic components and transposable elements in enabling organisms to rapidly produce new phenotypes and genotypes in response to stresses (Clegg & Durbin, 2000; Rey *et al*., 2016). Polyploidy thus enables new genetic variability upon which natural selection can operate leading to speciation. Many investigators consider the remarkable diversity of angiosperms to be due to the impact of polyploidy (Tank *et al*., 2015; Pelé *et al*. 2018; Levin, 2019). Polyploids also show more ecological tolerance and invasiveness when compared to their diploid progenitors (Levin, 2019). Several cultivated species such as *Triticum aestivum, Avena sativa, Arachis hypogaea, Nicotiana tabacum, Solanum tuberosum, Coffea arabica* and several species of *Musa* and *Brassica* have been shown to be polyploids (Hilu, 1993; Wickens, 2001).

Autopolyploidy: Spontaneous autopolyploids (organisms containing more than two complete and identical sets of chromosomes derived from the same species) often occur in populations of diploid species. Polyploids are reproductively isolated in one step. Pollinations between diploids and polyploids result in more or less sterile triploids and do not survive in the population, except where the main reproductive strategy revolves around vegetative propagation (*e.g. Curcuma*; Leong-Škornicková *et al*., 2007). Reproductive isolation between parental diploids and polyploids is largely confined to post-fertilization barriers. Polyploids with even chromosome sets (*e.g.* 4*x*, 6*x*, *etc*.) are fertile, tend to be more vigorous and withstand environmental stresses better than parental diploids; they are likely to increase in the population over time and may eventually replace the diploid plants in the populations (Levin, 2019). Despite the strong and imminent one step reproductive isolation between parental diploid and polyploid 'species', taxonomists may not be able to recognize recent autopolyploids as new species because morphological differences in most of them are too subtle to describe them as new species. Morphological differences have to be reinforced in polyploids through mutations to be able to bring about clear cut phenotypic changes, which may take some time, before taxonomists erect them as new species. This is one of the reasons for the delayed recognition of species resulting from autopolyploidy. Autopolyploidy has given rise to many wild as well as cultivated species such as potato and some of its relatives (Grant, 1981) and several species in Saxifragaceae (Soltis & Rieseberg, 1986; Wolf *et al.*, 1987; Soltis *et al.*, 1989. Many autopolyploid ginger varieties with improved quality have been produced (Smith *et al.*, 2004; Wei *et al.*, 2011).

Hybridization

Hybridization is another mechanism that drives speciation in plants (*e.g.* Mallet, 2007; Soltis & Soltis, 2009). The disruption of physical barriers between previously isolated congeneric species in which reproductive isolation is weak or has not yet evolved fully would allow the formation of hybrids. As pointed out earlier, reproductive isolation even between well recognized sister species is not absolute; some hybrids are produced when the populations of two closely related species come together permitting pollen flow between them. But most of the hybrids may not persist because of sterility and fitness problems but some of them, particularly those with vegetative propagation strategy may persist and evolve into a new species (Leong-Škornicková *et al.*, 2007).

There are two types of hybrid speciation. One is homoploid hybrid speciation in which the hybrids evolve into new species without a change in their chromosome number. The other is allopolyploid hybrid speciation which refers to the origin of new species through duplication of the hybrid genome.

Homoploid hybrid speciation: This mode of speciation is rarer than the allopolyploidy mode; as pointed out earlier, hybrids are generally sterile and also show often reduced fitness, particularly in early generations (but see Yang *et al.*, 2019). However, if they colonize new habitats, particularly those that are not congenial to the parental species, hybrids are likely to show better fitness and successfully establish in new habitats (Campbell & Waser, 2007). Thus, homoploid hybrids are largely reported in novel habitats that are not occupied by parental species. Several homoploid hybrids have been described (Gross & Rieseberg, 2005; Soltis & Soltis, 2009; Yakimowski & Rieseberg, 2014). Only a few are mentioned here. In *Helianthus*, *H. annuus* occupies soil that is rich in clay while *H. petiolarius* colonizes sandy soils. It has been shown, based on molecular evidences that three species of *Helianthus*, each occupying ecological divergent habitats, – *H. anomalus* (sand dune), *H. deserticola* (desert) *and H. paradoxus* (salt marsh), – have evolved through hybridization of *H. annuus* and *H. petiolaris* through homoploid speciation (Rieseberg, 2006; Buerkle & Rieseberg, 2008). *Senecio squalidus* derived from *S. aethnensis x S. chrysanthemifolius* is another homoploid hybrid (James & Abbott, 2005). In the above examples, ecological selection (because of the increased colonization potential of the hybrids) seems to have played a major role in homoploid speciation. Even when the hybrid comes in contact with the parental species that permits pollen flow, the hybrid remains as distinct species; it may not result in the new hybrid progeny because of sterility.

Allopolyploid hybrid speciation: Allopolyploid hybrids are usually fertile when they have an even number of genomes, and genome-wide changes in newly formed allopolyploids induce novel phenotypic and genotypic variations which are likely to contribute to the survival and ultimate success of allopolyploids. Alloploid hybrid speciation is more common than homoploid hybrid speciation and there are a number of examples (Wood *et al.*, 2009; Levin, 2019). Several crops and ornamental species have been shown to be of alloploid origin. Some other reports of allopolyploid species include: *Mimulus peregrinus*, an allohexaploid (6*x*) hybrid species between *M. guttatus* (2*x*) and *M. luteus* (4*x*) (Vallejo-Marín, 2012). Similarly, *Nicotiana tabacum* is an allotetraploid hybrid species between *N. sylvestris* (2*x*) and *N. tomentisiformis* (2*x*) (Sheen, 1972).

As pointed out earlier, speciation in general is a slow process and may take hundreds of generations. However, speciation through polyploids, especially allopolyploids are exceptions in the sense that new recognizable species are formed in one or few steps. However, natural selection acts on their sustainability and spread which may take a number of generations during which they undergo many genetic and epigenetic changes in relation to natural selection. Although a large number of hybrid species are formed due to incomplete reproductive isolation of parental species, most of them do not survive and fail to evolve as new species.

Outlook of speciation in the Anthropocene era

Research and discussions on speciation in flowering plants would, no doubt, continue to be intense in the coming years and the emerging technologies in analytical methods may allow us to study speciation in greater detail. One of the major concerns of human-induced environmental changes including the climate change in recent decades has been its impact on biodiversity. A general consensus amongst conservation biologists has been that as many as one third of species may become extinct by the end of the century which is thousands of times more than the background extinction rate (Barnosky *et al*., 2011; Ceballos *et al*., 2020; IUCN, 2020). According to IUCN (2020), 27% of all assessed species are threatened with extinction. Most of the assessed groups, however, belong to animals. More importantly a large number of species may not become extinct but their population densities and geographical distribution would be reduced to such an extent that they are unable to make any impact on community interactions (see Pimm & Raven, 2019; Ceballos *et al*., 2020; Raven, 2020). According to some biologists, plant species seem to be comparatively resistant to extinction when compared to animal species (see Vellend *et al*., 2017). However, amongst the limited plant groups assessed by IUCN, 34% of the conifers are reported to be threatened, which is more than many of the threatened animal groups. In a recent detailed study, based on a comprehensive global analysis, Humphreys *et al*. (2019) documented extinction of about 600 plant species since 1900 (excluding species which were declared extinct but were subsequently rediscovered); this amounts to a 500 times higher than the background extinction rate (see also Ledford, 2019). According to their analysis species on islands and in the tropics particularly those with narrow distribution ranges are more susceptible (Humphreys *et al*., 2019). The general outlook from the discussions on human-induced mass extinction is that the biodiversity on the planet is going to be markedly reduced in the coming decades.

However, the prevailing biodiversity (both described and un-described) depends on the proportion of the number of species that become extinct to the number of new species formed. In contrast to the availability of enormous literature on species extinction, there is very limited discussion on the impact of climate change on speciation in the coming decades (Thomas, 2015; Bull & Maron, 2016; Vellend *et al*., 2017; Otto, 2018; Levin, 2019). A few authors have observed and expected an accelerated rate of speciation in the recent past and coming decades, often referred to as Anthropocene, due to extensive ongoing human-induced environmental and biological changes (Thomas, 2015; Levin, 2019). According to Thomas (2015) the number of new species that have arisen in Europe over the past three centuries are more than the number of species documented as extinct during the same period; this increase has been the result of modern agriculture, horticulture and the human-mediated extensive transport of species across regions, followed by hybridization. According to Levin (2019, but see also Gao, 2019) auto- and allo-polyploidy are going to be the primary modes of speciation in the next 500 years and the proportion of polyploid species would surpass 50% amongst the described species. He argues that environmental stresses induced due to climate change are likely to trigger higher rates of speciation through mutations and other genetic changes. Equally important, not in relation to speciation but for the sustenance of human welfare, is the responses of crop species to the ongoing climate change (Gornall *et al*. 2010). Would climate change induce higher levels of polyploidy or other genetic changes in crop species in the coming decades leading to the evolution/development of new genotypes/varieties/species so that they are able to sustain productivity and quality of food grains? This is going to be important as it affects food and nutritional security of the increasing population of the world, particularly in developing countries.

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Appendix1: Some terminologies related to speciation

Phyletic speciation: One species gradually transforming into a new species by accumulation of variations. Phyletic speciation does not increase biological diversity as it does not increase the number of species.

Divergent speciation/Cladogenesis: One species giving rise to two or more species and thus results in phylogenetic branching of the species. All the species resulting from cladogenesis may exist at a given time or any of them may become extinct at some point. Cladogenesis increases the number of species and thus biological diversity.

Phylogenetic tree: Is a diagram that shows an inferred (from fossil, and morphological and molecular evidences) path of evolution and evolutionary relationships between species. The node in a phylogenetic tree represents the common ancestor.

Sister species: Sister species are the two species derived from a common ancestral node. They represent each other's closest relatives since they share an ancestral species not shared by any other species.

Clade: A clade is a monophyletic group of organisms that includes all descendant species from a common ancestor (both extinct and extant).

Adaptive radiation: Speciation in which a species diverges rapidly into many species in comparatively a short time. This generally happens when a species enters a new habitat where there is little or no competition or environmental stress. Speciation through adaptive radiation is common in volcanic islands. When one or a few seeds arrive on these islands from the mainland, the initial population (founding population) is made up of an extremely small gene pool. The plants are free from predation by herbivores and of pathogens or from competition from other plants. The population multiplies rapidly and builds up the gene pool. When they spread to neighbouring islands, the populations of each island adapt to local conditions and evolve into new species.

Some examples of adaptive radiation: The Hawaiian group of silverswords consists of twenty eight species under three genera, *Debautia* (21 species), *Argyroxiphium* (5 species), *Wilkesia* (2 species), which include trees, shrubs, vines and cushion plants occupying different habitats. All available evidences indicate that all species of this group are the descendants from one species that arrived on Hawaiian islands millions of years ago (Baldwin & Sanderson, 1998). Another remarkable example of adaptive radiation is the species of *Drosophila* on Hawaiian Islands (Zimmerman, 1970; Ashburner *et al.*, 1981). Over 500 species of *Drosophila* are estimated to be present on these Islands and evidences indicate that all of them have evolved from one or two original founder individuals. Fifty six species of honeycreepers (birds) on Hawaiian Islands, (some of which have become extinct) (Olsen, 2004) and 14 species of Darwin's finches on Galapagos Islands (Petren *et al.*, 2005) are also well known examples of adaptive radiation.

Genetic drift: Genetic drift is a random process that leads to large changes in the allelic composition of populations over a short period of time. Many of the alleles may get eliminated from the population irrespective of their role in the fitness of individuals. A few individuals of the population that survive may start recovering but their allelic composition would be different from the original population.

Ecotype: An ecotype is a genetically distinct geographic variant/population/race of a species which is adapted to specific environmental conditions. Phenotypic differences of ecotypes are of minor nature or too subtle to warrant classifying them into subspecies. Ecotypes are able to interbreed with other ecotypes without the loss of fertility or vigour.

Microevolution: Genetic variations in the population leading to the evolution of new varieties and species through selection of individuals or random drift.

Macroevolution: Evolution of taxonomic hierarchy above species levels (families, orders etc.) that evolve over millions of years.