

Rajesh Tandon
K. R. Shivanna
Monika Koul *Editors*

Reproductive Ecology of Flowering Plants: Patterns and Processes

 Springer

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*Dedicated to
Professor H.Y. Mohan Ram*

Foreword

Higher plant reproduction is important as it sustains life on this planet. All cereals, millets, pulses, nuts, and oil seeds are products of plant reproduction. It is, therefore, no wonder that constant human endeavor has gone into understanding different aspects of flowering plant reproduction through field and laboratory experimentation. Plant reproductive ecology is comparatively a younger field. Yet, on account of its importance, it has attracted wide attention of biologists pursuing diverse fields.

Successful accomplishment of plant reproduction depends heavily upon compatibility of plants with biotic and abiotic components of the environment they live in. The importance has increased manifold following changes caused in environment by anthropogenic pressures.

A lot of information on reproductive ecology has been generated in recent years. For want of a journal or book solely devoted to this subject, it is scattered and, therefore, not handy to researchers pursuing this aspect of plant reproduction. This volume will fill this long-felt need.

Edited by three eminent biologists who have themselves contributed richly to unravel the mysteries of plant reproduction, the book comprises 16 chapters. Each chapter is authored by well-grounded author/authors in the subject.

The book makes for an absorbing read, as it presents systematic and lucid account of what reproductive biology is all about and in what way plant reproduction is linked with ecology. Students of botany and evolutionary biology will find latest information on floral symmetry, nectary, pistil, and secondary pollen presentation in the book. Plant breeders and crop geneticists will be enriched by Chaps. 8, 11, 12, 13, and 15. Chapters 2, 14, and 16 are of wide interest, focusing on the impact of climate change, the availability of pollinators and seed-dispersing birds, and the accomplishment of plant reproduction. As it is, the book will benefit a wide spectrum of biologists.

The book is well written, with suitable illustrations, wherever required, to help the readers. It will also help develop greater interest for plant reproductive ecology among biologists.

Former Professor of Botany, Jammu University
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January 3, 2020

A. K. Koul

Preface

Plant reproductive ecology has emerged as one of the most versatile and important fields of plant sciences. It answers two basic questions relevant to the survival of plant species: First, how do plants reproduce to sustain their populations? And second, how do plants strategize to escape reproductive failure? Considering the enormous diversity of plant species and their habitats, significant amount of variation is expected in the ecological processes that facilitate their reproductive success. Furthermore, the scales at which the processes become evolutionarily tenable also vary over successive generations of plants. Over the years, these aspects have been explored and understood at different levels of organization to answer specific questions. In recent years, the progress of the subject has been stimulated by growing interdisciplinarity to address the key global issues of ensuring future food security and conservation of biodiversity in the light of human-induced environmental changes, particularly climate change.

This is an area that has attracted a large number of laboratories around the world, and enormous new knowledge is being generated. The vast information generated in the subject is mostly scattered among journals. Though there are books by experts on the subject focusing on flowering plants, they largely deal with specialized areas of reproductive biology. The need for an updated, comprehensive book that does not represent conventional presentation of information has been felt time and again by reproductive ecologists. Although the information in this discipline is too vast to compile into a single volume, this book tries to highlight some of the fundamental processes and patterns linked to plant reproduction. The focus has been to synthesize and use the information that is available for greater understanding and interpretation of the ecological processes governing reproduction.

Reproductive ecological database broadly includes the details of flowering phenology, floral biology, pollination mechanism, pollen-pistil interaction, breeding system, and natural recruitment. Chapter 1, authored by the editors, is an overview on these key aspects and some of the noticeable dependencies associated with them. However, variations may arise depending on species. Chapter 2, authored by Saxena and Rao, highlights the potential of plant phenophases in understanding global climate change. After providing a conceptual background on the topic, it also highlights the key gaps in the knowledge and illustrates some pertinent examples on the issue.

Chapters 3 and 4, authored by K.R. Shivanna, briefly highlight the structural details of the pistil including that of the embryo sac in relation to its function. Besides the structural diversity of stigma, style, and ovary, these chapters also elaborate upon physiological and biochemical features that govern the dynamics during the pollen-pistil interaction, and provide information on extracellular substances that play a role in intercellular interactions at various levels prior to and during fertilization.

Pollination is an important event that decides the generation of a progeny. It is facilitated by both biotic and abiotic factors. Enormous literature has accumulated on various facets of pollination over the years. As is becoming clear by both field and laboratory studies, plant-pollinator interactions are governed and mediated by various cues. Chapter 5, authored by Sashidhran and Venkatesan, updates on current knowledge about floral volatiles (olfactory cues) as a functional trait for plant reproduction. It also discusses in detail an account of diverse functions of floral volatiles, their chemical nature and biosynthesis including the regulation of their emission by biotic and abiotic factors.

Chapter 6, contributed by Phukela et al., gives an overview of the distribution of floral nectaries along with a brief account on the genetic switches that regulate nectary development among flowering plants. By mapping the distribution of nectaries on angiosperm phylogeny, the authors trace the evolutionary history of nectaries across angiosperm lineages and discuss the role of nectary as a key functional trait in pollination.

Chapter 7, by R. Geeta and Eapsa Berry, provides a stimulating account on floral symmetry, the facet that is variable in angiosperms as polysymmetrical, disymmetrical, and monosymmetrical forms. The authors discuss reasons behind the variation and role played by ecological interactions of flowers with biota, especially with pollinators, which may exert selection to favor one or the other symmetry state. On the basis of phylogenetic analysis, the authors also look at the evolution of symmetry and how it may get compromised in plants.

Resource allocation and optimization strategies are important as these favor natural selection and maximize plant fitness to the prevailing biotic and abiotic stresses. Chapter 8, by Kumari et al., shows that resource allocation and optimization are regulated by life-history patterns and breeding system of the species to ensure the development of a viable progeny. The authors give information on various theories prevalent on resource allocation and partitioning and also discuss the methods used to quantify resources allocated for reproductive effort citing various examples from their research work.

Dioecy, characterized by the presence of distinct male and female plants, is relatively rare in flowering plants and is an important mechanism that is accompanied by obligate outcrossing. Chapter 9, contributed by Mangla et al., explains the role of various ecological factors which work in unison to shape dioecy in angiosperms. The authors discuss in detail the role of floral attributes, wind pollination, fruit type, clonality, and resource allocation which favor and help in the maintenance of dioecy.

The knowledge of floral attributes is important to understand the intricacy of reproductive mechanisms that are integral to establish successful plant-pollinator

interaction and maximize plant fitness. Chapter 10, authored by Barman et al., focuses on structural and mechanistic diversity of secondary pollen presentation among angiosperms. The significance of these methods mainly lies in the targeted deposition of pollen for successful mating. Chapter 11, authored by Kaur, dwells on the outbreeding patterns in angiosperms in detail and also highlights the diverse outbreeding packages that the flowering plants have evolved citing interesting examples. Moreover, it briefs on the plasticity in resource allocation in relation to the outcomes of sex differentiation in higher plants.

Sexual selection in plants is rarely discussed, as it has been more extensively investigated in evolution of animals for their better adaptability to choose traits for mate. Chapter 12, by Kaul and Raina, gives a succinct account on how sexual selection occurs in plants. After providing a brief historical perspective on the issue, it discusses various theories, conceptual developments, and roles of various traits associated with sexual selection in plants.

Apomixis is an asexual mode of reproduction through seeds wherein meiosis and fertilization are bypassed. Chapter 13, contributed by Sharma and Bhat, is a crisp and consolidated information on this very important topic. The authors trace the origin of apomixis citing various types and variations found in angiosperms, especially grasses. While earlier the apomictic lineages were considered to be a dead end, the authors indicate that current understanding treats them as a means of diversification of polyploid complexes in angiosperms.

Frugivore animals are known to have played a crucial role in the evolution of seed dispersal mechanisms. Chapter 14, by Sinu et al., provides an interesting account on the role of endozoochory through birds, bats, and fishes, especially in long-distance dispersal of seeds. It then discusses in detail about the complexity of ecological drivers that materializes the dispersal and points out the present-day threats to this important mutualistic interaction in the tropics.

The widespread global adoption of transgenic plants has been controversial and has raised concerns regarding the transgene flow. Chapter 15, authored by Lal et al., comprehensively deliberates on most of the pertinent aspects of transgene flow including the biosafety concerns. It also highlights the details of alien genetic elements introgressed into the genome of weedy and wild species through transgene flow from crop species and how they confer selective advantage in some species. The approaches that need to be adopted and the analytical methods and mitigation strategies to be followed to contain harmful impacts are explained. Furthermore, the chapter also discusses in detail studies carried out on some of the selected crop species such as maize, rice, and mustard.

Chapter 16 is on the present-day challenge posed by pollinator decline. Authored by the editors, K.R. Shivanna, Rajesh Tandon, and Monika Koul, this chapter highlights major concern over loss of pollinators, particularly in the tropics. It discusses the details of drivers for pollinator decline across the globe and points out as to how anthropogenic activities are the major culprits and the need for mitigation of the crisis. It also highlights the close linkage between the pollinator crisis and food and nutritional security of the growing population.

This book is a tiny tribute to Professor H.Y. Mohan Ram, one of the most passionate teachers of botany in India. He was an ardent propagator of botanical knowledge. We are sure that this volume would be of interest to teachers and researchers in both the basic and applied fields of plant sciences including agricultural scientists, foresters, and conservation biologists.

It is a privilege to thank all the contributors who have made this book a reality. We appreciate Yash Mangla, Vineet K Singh, Banisha Phukela, Arjun Adit, Sachin, and Manisha for their willingness to help during the finalization of this edited volume. Our warm appreciation goes to the Springer team for their constant support and comradeship.

New Delhi, Delhi, India
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New Delhi, Delhi, India

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K. R. Shivanna
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Monika Koul is presently working as an Assistant Professor in the Department of Botany, Hansraj College, University of Delhi. She did her Ph. D. in Botany from the University of Delhi in 2004. She is involved in teaching of Reproductive Biology of Plants and Ecology to the undergraduate students of Botany, Zoology and Life Sciences for last 14 years. Monika has published 12 research papers, written a number of popular science articles in magazines and contributed chapters in various books. She has also co-edited one book and written articles for national newspapers on topics related to environment and conservation. Monika has also been a resource person for teacher training workshops and participated in developing e-content in NCERT and CBSE. She is the recipient of Ramaseshan Fellowship and SRF from Current Science Academy, IASC Bangaluru, India.

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Reproductive Ecology of Flowering Plants: An Introduction

1

Rajesh Tandon, Monika Koul, and K. R. Shivanna

Abstract

Sexual reproduction is vital to ensure variation and perpetuation in organisms. In flowering plants, the reproductive process is accomplished in four major phases. The first phase encompasses the development and organization of flowers, the second ensures pollination, the third includes events leading to fertilization and seed formation and the fourth is defined by dispersal of seeds and their recruitment in populations. Plants optimize reproductive success through interaction between these components of reproductive system and ecological factors. Longevity, vitality and sterility of sexual systems have been well understood in wild and crop species and studies on these aspects have unravelled interesting patterns in angiosperms. However, there is paucity of information on certain aspects such as how plant species modify their reproductive functions in varied habitats and how sexual systems respond to evolutionary pathways, and environmental cues. Reproductive ecological studies are currently trying to answer these questions, as reproductive processes operate in continuum with environmental variables and show specific responses and patterns. These studies also help in understanding the trade-offs and constraints that the angiosperms are always confronted with. The present chapter highlights some of the crucial aspects of reproduction covering phenology, floral biology, pollination ecology, breeding strategies and recruitment pattern. Elucidation of these processes is of immense importance in the management of forest ecosystems, recovery of threatened plant species and sustenance of yield in crops.

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Keywords

Phenology · Floral biology · Pollination ecology · Seed dispersal · Natural recruitment

Reproduction is a crucial step in the lifespan of organisms, which ensures their perpetuation as a distinct species. The success of the process is largely influenced by two components – the inherent biology of organisms and the ‘interactive’ ecological domain in which they grow and flourish. For plants, the second component becomes strongly decisive as it influences almost every step of reproduction. This is primarily due to immobile nature of plants, and therefore it is likely that reproductive success among them can be potentially constrained by any of the attributes of their multivariate environment in which they grow.

In flowering plants, the intricacy of the reproductive process, especially by sexual means, usually assumes a higher level by having numerous reiterative modules (*ramets*) in the same plant (*genet*). Such an organization of the plant body among angiosperms has fitness consequences – the prominent being the greater chance of self-interference. However, plants are equipped with devices and mechanisms to promote outcrossing (Lloyd and Webb 1986, Richards 1997). These devices (*barriers of selfing*) can be morphological, physiological or genetic in nature. In spite of the outbreeding advantages, there is no dearth of plants which follow selfing (~20% *autogamous*) in nature. In the eco-evolutionary context, outbreeding packages better competitive propagules than that from selfing. On the other hand, selfing offers stasis and assures survival (*reproductive assurance*). The questions arise: Why are a great majority of angiosperms inclined to *cosexuality* and bear both the genders either in the same flower (*bisexuality*) or on the same plant (*monoecy*)? One plausible explanation in favour of the predominance of cosexuality is that plants can avoid a separate investment for promoting male and female functions, by capitalizing on resources already allocated to attract the pollinators (Givnish 1980; Charlesworth and Charlesworth 1987a). However, if the barriers are not strong enough, the modularity in plant architecture and proximity of sexual organs and overlapping of their functions (*incomplete dichogamy*, Lloyd and Webb 1986) would increase the chances of self-interference with detrimental effects. *Inbreeding depression* (reduced fitness) and *ovule discounting* (clogging of the stigma with self-pollen) are the two adverse consequences of selfing in preferential outbreeders (Charlesworth and Charlesworth 1987b; Holsinger 2000; Barrett 2002). Studies in recent decades have shown that there is reasonable flexibility in predominant attributes, and shifting to alternative strategies is possible to favour perpetuation and survival (Shivanna 2015). For example, self-incompatibility (SI) in many plants is not absolute (Nasrallah and Nasrallah 2014), herkogamy and dichogamy may diminish if outcrossing fails (Kalisz et al. 2012), and plants may have mutualistic interaction with more than one type of pollinator (Johnson and Steiner 2000). Plants capitalize on such trait variations for adapting new mechanisms for the reproductive success when they experience shift in conditions and colonize new environments.

Though plants cannot move, their migration can be visualised in context of thinning of population sizes at unfavourable sites and their expansion at relatively salubrious conditions. Smaller population size is unstable and susceptible to extinction. The natural process of local extinction of a species in a population is gradual and directly happens due to failure in recruitment of new plants at regular intervals. The failure may happen at any stage from events leading to fruit/seed set or recruitment. Habitat fragmentation and consequent shortage of ecological safe sites further hamper the process of regeneration. The problem is more acute in the case of endemics which have narrow ecological amplitude. Ecological requirements in some species are too stringent to ensure reproductive success on a regular basis. How plants manage to recuperate under such threatened ecological suites can be suitably understood by investigating the species-specific reproductive strategies in relation to their surroundings.

The ecological approach to investigate reproductive biology of plants gives a perspective of populations and communities. One may look into the reproductive strategy of a species at different levels of organization from individual plants to their entire range of distribution. The information generated, in fact, strengthens the inferences by providing a wider perspective and reasoning on how developmental attributes are governed. For example, low seed or fruit set in a species may be due to self-incompatibility. Alternatively, limited fruit/seed set may also occur due to asynchronous flowering, occurrence of more than one co-flowering species, insufficient flowering to engage pollinators, insufficient pollination, heterospecific pollen transfer, pollinator's absence, poor availability of compatible mates, or even as a consequence of conflicts (*trade-off*) in allocation for resources to various functions (Larson and Barrett 2000; Morales and Traveset 2008; *see* Chap. 8). Further, vegetative reproduction through propagules (*bulbs, corms, tubers, root suckers, bulbils*) in many species including crops is an advantage to escape failure in sexual reproduction and help them survive through clonal expansion. Agamospermy (*apomixis*), another mode of asexual reproduction, harnesses the benefit of packaging clonality by seeds for distant dispersal and can be part of gene flow (*see* Chap. 13). All these dimensions in a way are decisive in determining the fate of progeny, composition of genetic structure of population, consequent gene flow pattern and many other processes that contribute to patterns on a larger scale for the species to maximize fitness. Reproductive ecological studies thus essentially incorporate 'elucidation of all aspects of reproductive events and their interactions with the biotic and abiotic components of the environment' (Shivanna and Tandon 2014). The list of microevolutionary processes driven by variability in heritable traits leading to different outcomes of mating patterns is far from complete as evolution is a continuous process. It justifies the continuous endeavour to unravel them in multifarious contexts. On account of brevity, we have highlighted a few of these.

1.1 Flowering Phenology

Life history stages are usually adaptive and are selected for features such as timing, duration and periodicity in relation to climatic factors (Rathkey and Lacey 1985). Flowering, a key life history event, is a subset of sequence of events (*phenoevents*) which responds to suitable signals from the environment; the other phenoevents include flushing of new leaves and their subsequent fall, fruiting and dispersal of *diaspores* (fruits or seeds) after maturation. The sequence of appearance of leaves before or after flowering can influence the manner in which flowers are presented for enhanced visibility and accessibility.

Recording various features of flowering pattern in a species over a period helps in identifying their discrete contribution to overall reproductive success (Richards 1997; Frankie et al. 1990). A species is considered to be in flowering if more than 50% of the individuals in the population are in bloom (Stiles 1978). Besides the above features, synchrony of flowering among the plants in a population has a significant influence on the mating pattern. Many a times, the inherent genetic variation among the individuals in a population may also cause out-of-phase blooming (Bullock and Bawa 1981; Opler et al. 1980). The flowering patterns may vary depending upon whether the plants flower en masse (*big bang*, *cornucopia*, *multiple bang*) or in extended phase (*steady state* or *modified steady state*) in a population (Gentry 1974). These patterns influence the constancy and foraging behaviour of pollinators. For example, in self-compatible *Strobilanthes kunthiana* (Acanthaceae), in the Western Ghats of India, flowering occurs in a big-bang pattern for short duration and after a regular gap of almost 12 years. The sudden enriched floral resource attracts *Apis cerana indica* which develops *constancy* and effects pollination. The plants are able to escape reproductive failure through gregarious flowering which enhances pollination efficiency and counters the effects of geitonogamy (Sharma et al. 2008). However, such a pattern is likely to differ with fluctuation in the intensity of flowering, as it is known to vary during different flowering seasons in the species. This may directly influence the relative proportion of the sired self- and cross-progeny. In bat-pollinated plants like *Oroxylum indicum* (Bignoniaceae), the long *steady-state* flowering (6–8 weeks) helps in establishing the fidelity to the pollinator type in different regions of their occurrence (Vikas et al. 2009). Bats are most conducive for pollination success as their trap-line foraging behaviour helps in ensuring outcrossing (*xenogamy*) in this obligate self-incompatible tree species. The flowers in *O. indicum* are short-lived and open acropetally in the long protruding and exposed inflorescence. Here, the direction of the opening of flowers within the inflorescence also becomes a crucial factor to permit the bat of only proper mass to be able to forage and fly away with ease. The reverse of this would be highly demanding for the constancy or even mutualism to establish. Similarly, the direction of the opening of flowers in the capitula of cheiropterous *Parkia* spp. (Fabaceae) has been shown to influence the presentation of nectar to the foragers on a spatio-temporal scale. In co-occurring bat-pollinated *Parkia* species, phenological separation through different timing of flowering has been shown to reduce competition for pollinators (Hopkins 1984).

As the phenological patterns are sensitive to climatic conditions, consistent minor changes in ambient temperature are likely to impact the phenological patterns (Easterling et al. 2000, Abu-Asab et al. 2001). The impacts would also cover community structure, composition and ecosystem functioning (*see* Chap. 2). Flowering stimulus is controlled and co-ordinated through external factors such as light, temperature and humidity. Photoperiod, quality and intensity of light all play a significant role in perception of flowering stimulus. Among these, increased ambient temperature is implicated to be the major causal factor in shifting the flowering phenology (Sherry et al. 2007). In the absence of systematic phenological records, it is difficult to ascertain the impact on natural vegetation. However, in species for which reliable records are available, significant shift in the onset of flowering dates has been recorded as in *Prunus jamasakura* by 7 days (Primack et al. 2009), in *Robinia pseudoacacia* by ~8 days (Walkovszky 1998) and in *Rhododendron arboreum* by 97 days (Gaira et al. 2014).

These observations on phenological patterns give information on the plasticity of key life history traits known and the putative developmental changes through epigenetic modifications that might follow (Hedhly et al. 2008). For example, the expression of *FLOWERING LOCUS C (FLC)* gene involved in the vernalization pathway is epigenetically regulated to induce flowering in *Arabidopsis thaliana*. The gene has been shown to successfully act as a quantitative tracer of the fluctuating temperature in *Arabidopsis halleri* (Shimizu et al. 2011). Such approaches may be employed for the focal species along the ecological cline to gather clues on the epigenetic changes that are accompanied by climate change-induced phenotypic variations.

1.2 Floral Biology

Flower is the fundamental unit of sexual reproduction. The timing of the opening of a flower (*anthesis*), the onset of stigma receptivity and the duration of pollen availability within a flower are the key features of floral biology. These attributes determine the longevity of the flower and correlate with the breeding and pollination mechanism.

For maximizing fitness, flowers may adopt various means to enhance export of pollen (*male fitness*), so that they may reach as many conspecifics as possible to ensure seed formation (*female fitness*) (Sutherland and Delph 1984). In order to achieve this, plant species optimize the timing of their functions in such a way that they coincide with the availability of mates and pollinators. Floral display (*colour, shape, size, olfaction*), their presentation in the plant (solitary or in an inflorescence; *enantiomorphy*), longevity, anthesis time, relative positions (*herkogamy*) and timing of maturation (*dichogamy*) of essential organs, presentation and type of rewards are some of the prominent floral functions that determine the potency of advertisement to attract pollinators (Waser and Price 1981; Mitchell et al. 2009 *see* Chaps. 5 and 7). Many of these traits are believed to be influenced through selection imposed by the pollinators (Parachnowitsch and Kessler 2010).

The timing of anthesis is important to understand floral biology and varies among taxa to exploit the pollinators according to their active period. Flowers that open during the daytime (*diurnal*) usually have display through colours of petals, while olfaction is the major cue for those that bloom during the night-time (*nocturnal*). The display size and arrangement of flowers further ensure the range up to which the floral cues may be captured by the potential pollinators during the day. Nocturnal flowers are predominantly white or dull in shades and are usually scented to attract pollinators in the night.

Usually the flowers open only once and senesce after pollination. However, in certain species, especially those with bowl or disc-shaped flowers, repeated cycles of opening and closure have been noticed (e.g. *Ipomoea*, *Silene saxifraga*). Such movements are attributed to physiological changes in response to light intensity in diurnals or by an increase in relative humidity among the nocturnal plants (see van Doorn and van Meeteren 2003). In temperate and arctic environment, temperature within the floral space conferred by its shape can strongly influence the visitation of pollinators (e.g. *Dryas integrifolia*, Rosaceae) and therefore the reproductive success (Kevan 1989, Dyer et al. 2006). In the tropical diurnal weed, *Volvulopsis nummularium* (Convolvulaceae), flowers open partly under lower temperature on rainy days and give an opportunity to the terrestrial snails (*Lamellaxis gracile*) to pollinate rather than to *Apis cerana indica*, which are more effective on bright sunny days (Sarma et al. 2007).

The blossom shape and size are perhaps the most co-adapted floral traits investigated in predicting the mutualistic partners (Faegri and van der Pijl 1979). Phenotypic matching between the flower and pollinators determines the legitimacy required in pollen transfer. Many examples have been cited in literature to demonstrate that how specialization is derived by the matching of phenotypic traits (Balducci et al. 2019). The best example is that of plants with long nectar spur and the matching mouthparts of nectar-feeding animals such as moths and bats (Darwin 1862; Muchhala and Thomson 2009). In orchids, including that of Darwin's *Angraecum sesquipedale*, the matching establishes as a result of directional selection for flowers with deep-seated nectar (Alexandersson and Johnson 2002). Similarly, *lock-and-key* mechanism has been suggested to be operational in the pollination success of *Oroxylum indicum*. In Thailand, the flowers of the species were shown to be essentially pollinated by *Eonycteris spelaea*, and in the similar manner by *Cynopterus sphinx* under Indian conditions (Gould 1978, Vikas et al. 2009).

Like the display size, longevity of flowers also has consequences on attracting pollinators and their frequency of foraging visits (Mathur and Mohan Ram 1978; Shivanna and Tandon 2014). It usually refers to the duration up to which flowers retain their freshness under field conditions (Primack 1985), but more precisely to the duration up to which the flowers are able to disperse or receive pollen (Shivanna and Tandon 2014). The duration may vary among species from few hours to 8 weeks, e.g. *Malvastrum coromandelianum* (2 h), *Tribulus terrestris* (4 h, pers. observ.), *Oroxylum indicum* (10 h, Vikas et al. 2009), *Kigelia pinnata* (2–3 days, Harris and Baker 1958) and orchids (up to 2 months, Schoen and Ashman 1995). Long-lived flowers can amply compensate for low pollinator visitation rates in

pollinator-limited environments to ensure sufficient receipt and promote pollen export (Arroyo et al. 2017). According to Ashman and Schoen (1994), floral longevity is a heritable adaptation that balances rates of pollen receipt and removal against the cost of floral maintenance which can be optimized by selection in nature.

The female and male phases in a flower are determined by the onset of stigma receptivity and anther dehiscence, respectively. The proximity, duration and overlapping of the two phases drive selection on the plant to dissuade and restrict self-interference. This may be achieved by separating the overlap either in space (*herkogamy*) or time (*dichogamy*) (Lloyd and Webb 1986; Webb and Lloyd 1986; see Chap. 11). Interestingly, both the modes are represented among the self-compatible as well as the self-incompatible plants (Takebayashi et al. 2006; see Kissling and Barrett 2013). This suggests that the traits are plastic and modifiable through minor developmental changes. Depending on the efficacy of the mechanism, either of the modes may be preferentially selected in a species (Webb and Lloyd 1986). For example, herkogamy has been demonstrated to be more effective than dichogamy in *Epimedium* (Berberidaceae), and it need not be necessarily accompanied by dichogamy to prevent self-interference in the species (Li et al. 2013). On the other hand, plasticity in the traits might be exploited by the species to adopt an alternate strategy while colonizing new environments. For example, in *Blackstonia perfoliata* (Gentianaceae) with minor temporal shift in the male phase, the breeding system has been shown to shift from delayed selfing under pollinator-rich conditions to competing selfing in recently established populations (Brys and Jacquemyn 2011). In *Utricularia praeterita* and *U. babui* (Lentibulariaceae), failure in cross-pollination (*due to pollinator limitation*) leads to loss in herkogamy (*diminished herkogamy*) at the later stages of opened flower, and the elongation of stamens causes autonomous delayed selfing in the species (Chaudhary et al. 2018).

The incidence of dichogamy among plants varies in the context of separation of sexual function within or between the flowers. *Protandry* (maturation of anthers prior to stigma) is more common (~66%) than *protogyny* (~33%) at the intrafloral level, and the reverse is true for the interfloral level with greater incidence (77%) of protogyny (Bertin and Newman 1993). Further, dichogamy besides preventing self-fertilization also prevents self-interference during the *progamic* (pollen-pistil interaction) phase and synchronizes pollen release and stigma receptivity in the different flower types.

1.3 Plant Sexuality

Sexual expression in a plant is the representation of the predominant phase of a particular gender. The condition may involve *temporal* or *spatial* separation of the exchange of gametes among the individuals in a population (see Renner 2014). It can be determined at the level of a flower, individual plant or the population (Shivanna and Tandon 2014). In contrast to the hermaphroditic plants with bisexual flowers (~70%), the proportion of plants with sexually dimorphic conditions is limited

(Barrett 2002). Only 6% of the taxa are known to exhibit *dioecy*, a condition which has been derived from cosexuality on numerous independent occasions (Westergaard 1958; Charlesworth 2002). Unlike taxa with temporal separation of gamete exchange, those with spatial separation mechanisms, especially dicliny, monoecy, trioecy, androdioecy and gynodioecy, appear to have direct link with evolution of dioecy (Renner et al. 2007; Renner 2014). In spite of their low proportion, dioecious taxa have a considerable occurrence range and their distribution pattern correlates with some of the key ecological features (see Chap. 9).

Sterculia urens (Malvaceae) is a commercially important gum (Indian tragacanth) producing deciduous tree species. The *andromonoecious* condition in the tree species is attributed to a greater proportion of the male than the functionally female bisexual flowers (*cryptic monoecy*). The red anthers in the bisexual flowers serve as a means of pollinator attraction (Sunnichan et al. 2004). Cryptic monoecy may also be recorded among taxa with temporal separation of genders (e.g. *Acer oblongum*) (Yadav et al. 2016).

The temporal patterns allow the same individual to behave as male or female, and the proportion of individuals with different genders in the population influences their ratio. The sequence of sexual expression varies among taxa. For example, in Sapindaceae, most of the *Acer* species are known to exhibit temporal separation of genders (Renner et al. 2007). They are either *heterodichogamous* (two morphs that alternate with each other) or *duodichogamous* (the same morph behaves in the order as male, female and then again male); very few are dioecious. In oil palm (*Elaeis guineensis*, Arecaceae), the plants alternate in sex expression as male or female (*ontogenic sex change*) in the population, and their ratio can significantly influence the yield (Tandon et al. 2001a). It has been noticed that the nutrient supplementation in the Tenera hybrids (dwarf variety) of the palm is essential for the first three years of their plantation to maintain the seasonal sequence of genders; otherwise the plants behave as male throughout their lifespan. Such gender plasticity is known to be partly determined by resource status in some taxa (Diggle 1993).

1.4 Pollination

Pollination ecology is the most extensively investigated aspect of reproductive biology in flowering plants. The dynamics of plant-pollinator interaction have been used to explain several micro- and macroevolutionary processes, ranging from elucidation of reproductive strategy of a given species to gene flow, mating system, specialization of pollination syndromes and pollinator-mediated speciation. Most of these studies suggest that these processes are ecologically driven, at times can be context dependent, often highly diffused and yet vital for the survival of plants (Mitchell et al. 2009; Harder and Barrett 2006; see Barrett 2008; Sletvold 2019).

With increase in the awareness over a period of time, standardization of protocols, application of molecular tools, genetic approaches and availability of powerful software tools, a gamut of information has been generated on the subject. The

information has paved the way to test theoretical generalizations. Based on the information, some of the noticeable trends that have emerged are cited below:

- Entomophily is the predominant mode of biotic pollination across the planet, and the bees (tribe Apidae) are the most efficient pollinators. Wind pollination is secondarily derived among insect-pollinated taxa (Bronstein et al. 2006; Waser and Ollerton 2006; Friedman and Barrett 2008; Culley et al. 2002; *also see* Chap. 9).
- The notion that *pollination syndromes* (suites of convergent floral traits among unrelated taxa adapted to attract a particular functional group of pollinators) are important for predicting the mutualistic partners may not always hold true. In a specialized mutualism, the pollinators may belong to one functional group rather than to just one species (Faegri and van der Pijl 1979; Johnson and Steiner 2000; Tandon et al. 2003; Fenster et al. 2004; Ollerton et al. 2009).
- Bilateral symmetry; the quality, quantity and location of rewards in a flower; and cues of attraction (visual as well as olfactory) promote constancy and pollination efficiency. Many of them are also effective in filtering the antagonists (Williams and Dodson 1972; Baker and Baker 1983; Irwin et al. 2004; Junker and Blüthgen 2010; Singh et al. 2014; Tiedeken et al. 2016).
- Because of the obligate reliance of nearly 90% of flowering plants on a range of taxonomically unrelated biotic pollinators, their foraging behaviour largely influences the gene flow and mating patterns on a spatio-temporal scale (Levin and Kerster 1969; Nason et al. 1998; Karron et al. 2009).
- Networks of plant-pollinator interactions are mostly nested due to the preponderance of generalists rather than the specialists. Generalists impart strength, diversity and stability to the networks through numerous links, enhanced connectedness and low modularity (Bascompte et al. 2003; Olesen et al. 2007). High modularity in the interaction network is a feature of enhanced specialization, as in Bignoniaceae (Genini et al. 2010).
- Pollinators exert selection on floral traits to enable plants to adapt to new environments with suitable syndromes, resulting in speciation and diversification of taxa (*ecological speciation*) (Goodwillie et al. 2010; van der Niet et al. 2014; Dellinger et al. 2019). But the presence of antagonists like nectar robbers may mask the selection of the traits by pollinators, and many a times abiotic factors can also exert equal strength of selection (Harder and Johnson 2009; Caruso et al. 2019).
- Pollinator-mediated selection is driven through *geographical mosaics* of pollination landscape, spanned across the distributional range of a species (Van der Niet et al. 2014; Newman et al. 2014).
- Transitions in reproductive traits (e.g. floral colour, pollination syndromes, biotic and abiotic mode of pollination, self-incompatibility and sexual systems) are accompanied by modifications in the genetic systems and other related life history traits (*see* Barrett 2008).

In spite of its importance in sustaining crops, and conserving biodiversity and ecosystem services, pollination data from many regions, especially the tropics, is far from complete (Corlett 2004, Roubik et al. 2005, *see* Chap. 16). Considering that mutualistic interactions are diffuse and highly amenable to shifts, it is likely that the present trend of unstable climatic conditions may destabilize the fidelity of interactions. Intermittent reproductive failure in natural populations of plants is expected for a long period. Habitat modifications leading to fragmentation of vegetation would induce density-dependent demographic effects on mating patterns and trophic organization in plant communities.

1.5 Progamic Phase

The phase comprising events from pollination to fertilization is termed the progamic or the pollen-pistil interaction phase. Pistil is the key developmental innovation accompanied by angiospermy (*syncarpy*), the mechanism which concealed the ovules and the developing seeds to prevent predation. The mechanism also elaborated the maternal tissue for recognition or rejection of the male gametophytes (Endress 2001). Syncarpy is a predominant feature among angiosperms (~83%), while those with apocarpous pistils are usually seen among the basal angiosperms indicating that syncarpy evolved on multiple occasions (Endress 1982; Armbruster et al. 2002). Besides protection to ovules, the other advantages of syncarpy are attributed to greater precision in pollination, pollen-pistil interaction and efficient dispersal of seeds through adaptations of fruits (Armbruster et al. 2001). Pollen tube growth through the pistil serves as the site for competition among males and favours fertilization by most vigorous pollen resulting in better quality of seeds (Mulcahy and Mulcahy 1987, Shivanna 2003, 2011).

Innovation of pistil led to a significant shift in the manner the gametophyte selection occurs in flowering plants (*see* Chaps. 3, 4 and 12). The recognition and rejection of male gametes were taken over by somatic tissues of the pistil rather than by the gametes, as in the lower plants (Shivanna 2003; Bedinger et al. 2017). Flowering plants exhibit considerable diversity in the structural organization of the pistil (*see for the types* Heslop-Harrison and Shivanna 1977). The style primarily differs either by having a transmitting tissue tract (*solid-style*) or a stylar canal (*hollow-style*), while the stigma types differ on the basis of surface morphology and the ability to produce mucilagenous exudates once receptive (Chap. 3). The structural modifications in the pistil were superimposed by the physiological mechanisms that favoured outcrossing (Herrero and Hormaza 1996, de Graaf et al. 2001; Scutt et al. 2006). The attributes of the stigma surface usually correlate with the genetics of self-incompatibility; the sporophytic type (SSI) is associated with the dry type of stigma and gametophytic type (GSI) in most of the cases with the wet types (Shivanna 2003).

Another noticeable superimposition includes touch-sensitive nature of stigma, as seen in Lentibulariaceae, Scrophulariaceae, Bignoniaceae, Martyniaceae and Acanthaceae (Friedman et al. 2017; Chaudhary et al. 2018). The additional

mechanisms to prevent self-interference in the pistil can be transient and become effective only at the peak time of pollen presentation. For example, SI can be weak in the bud stage (Nasrallah et al. 2002, Shivanna 2003), and the sensitive lobes of the stigma may close permanently on single touch (Vikas et al. 2009). Such a developmental plasticity creates amenabilities for selfing to assume the role of reproductive assurance under pollinator or mate-limited environment as seen in *Utricularia*.

1.6 Breeding System and Mating Patterns

The breeding characteristics of flowering plants range from complete selfing (*autogamy*) to obligate outcrossing (*xenogamy*) (Bawa and Beach 1981; Richards 1997). In a population, the characteristics are driven by pollinator-mediated pollen flow and the extent of self-incompatibility among the conspecifics (Gan et al. 2013; Barman et al. 2018). Together these attributes generate a mating pattern which reflects the relative genetic contributions to subsequent generation (Wyatt 1986; Loveless and Hamrick 1984; Barrett 2003).

Self-incompatibility (SI), a feature common among plants with bisexual flowers (Bawa 1992, de Nettancourt 2001), is mainly a pre-fertilization barrier manifested through inhibition of pollen germination on the stigma or pollen tube growth in the style and differs *sensu stricto* from self-sterility (Barrett 1988). In the latter type, the fertilized ovules abort at various stages. Both the mechanisms lead to failure in seed set. Reproductive success in obligate SI plants (selfing rate < 20%, Zapata and Arroyo 1978, Schemske & Lande 1985) requires maintenance of a sufficient amount of allelic diversity and heterogeneity among the conspecifics. Delayed SI in which the pollen tubes are inhibited in the ovarian region has been reported in some species, and this is referred to as late-acting SI or LSI (Seavey and Bawa 1986; Gibbs and Bianchi 1999; Tandon et al. 2001b; Vikas et al. 2009).

In many plants SI is weak (*pseudo SC or partial SI*) and may permit some fruit set through selfing as well, making them preferential outbreeders (Bawa 1974, 1979; Tandon et al. 2001b; Good-Avila & Stephenson 2002). The extent of SI can be ascertained through usual bagging experiments (Shivanna and Tandon 2014). The approach has established that many plant species in the tropics are partially self-compatible or principally outcrossing (Bawa 1974; Tandon et al. 2001b; 2003). The relative proportions of selfed and crossed progeny sired are difficult to ascertain by routine bagging experiments alone; such studies need to be combined with suitable genetic markers to establish the extent of outcrossing rate (multi-locus t_m and single locus t_s), biparental inbreeding (t_m-t_s), correlation of paternity (r_s), gene flow pattern and even sexual selection by determining the pollen donors (Ritland and Jain 1981; Ritland 2002). Many tropical tree species (e.g. *Eucalyptus urophylla*, *Platypodium elegans*, *Shorea congestiflora*, *Warburgia ugandensis*) exhibit high ($t_m > 85\%$) outcrossing rates (Hamrick and Murawski 1990; Murawski and Hamrick 1991; Gaiotto et al. 1997; Muchugi et al. 2008). However, species with outcrossing rate between 50% and 80% belong to the mixed-mating category.

There has been a recent surge in studies demonstrating the increasing incidence of mixed mating among flowering plants. The case is more prevalent among the animal-pollinated species which show continuous variation in outcrossing index (Goodwillie et al. 2005). Variation may occur even within the same species and in different seasons and populations. Thus, the contributory variables for the success of mixed mating are context dependent (Schemske and Lande 1985; Holsinger 1991). There is a continuous debate on how such a strategy may evolve or be maintained in some species. The extent of biparental inbreeding (crossing between sibs), geitonogamy and inbreeding depression are some of the factors recognized that play an important role in the evolutionary maintenance of mixed mating (Uyenoyama 1986; Goodwillie et al. 2005). With the increase in biparental inbreeding, the genetic relatedness of the parents with the progeny also increases and promotes frequency-dependent selection to maintain intermediate outcrossing in a population (Uyenoyama 1986). Inbreeding depression, which plays a crucial role in mating system evolution, correlates with the selfing rates (Charlesworth and Charlesworth 1987b; Holsinger 1991; Winn et al. 2011). Geitonogamous selfing is an unavoidable feature common to plants with mixed-mating system as well as in those where autogamy is prevented (Eckert 2000). For example, the trees of *Wrightia tomentosa* (Apocynaceae) are self-compatible, but autogamy is not permissible due to architectural restrictions imposed in the flower – a feature conserved in the family for promoting outcrossing. However, geitonogamy mediated by the ‘settling moths’ has been shown to cause nearly 30% selfing among the trees (Barman et al. 2018). The other types of moths (hawkmoths) were responsible for xenogamy (~70%). The study has shown that besides the above-mentioned factors, pollination systems could also be crucial in driving and maintaining mixed mating in plant species.

The breakdown in self-incompatibility (SI) can set a course for the evolution of selfing, and such transitions have happened on numerous occasions among the flowering plants (Barrett 2002, Brandvain et al. 2014). Conditions that select for the evolution of self-compatibility include those which promote reproductive assurance and must be accompanied by gradual lowering in inbreeding depression (Shimizu and Tsuchimatsu 2015). Plants are believed to promote self-fertilization in harsher environments (Lloyd 1992). According to the *reproductive assurance hypothesis*, the selfing taxa are commonly associated with ephemeral and extreme environments where the availability of mates and pollinators both are limited (Cheptou 2012). Mixed mating can evolve into a complete selfing when plants colonize pollination-limited environment. However for the success of the shift in pollination, floral traits conducive for anemophily like small size of flowers with high pollen production should also evolve in synchrony (Shimizu and Tsuchimatsu 2015).

1.7 Dispersal and Natural Recruitment

Besides the pollen grains, seeds constitute the second important component of gene flow in angiosperms. Dispersal of seeds or fruits (*diaspores*) serves as an important link between the post-fertilization developmental events and the establishment of subsequent generation (*recruitment*). Like all flowers do not develop into fruits and all ovules do not develop into seeds, all seeds formed are not able to establish into a new plant. Such patterns emerge by developmental and environmental stochasticities working on the processes (Shivanna and Tandon 2014). Yet, it is important that the diaspores ought to be produced in optimal amount to ensure reasonable recruitment in the population (Stephenson 1981; Ghazoul and Sheil 2010).

For recruitment, it is the ecological framework which defines the operational success of a dispersal strategy and patterns. Like pollination, the success of dispersal also depends on a variety of dispersal modes – by animals (*zoochory*), wind (*anemochory*) and self-dispersal like explosive release of seeds (*autochory*) (van der Pijl 1982; Corlett 1998; Cousens et al. 2008; Shivanna and Tandon 2014). However, it is believed that some of the dispersal syndromes have proved insufficient to explain (i) the intricacies of long-distance dispersal mechanisms, including invasion, which may often involve more than one dispersal agents (*see* Chap. 14), (ii) range expansion of plant species and (iii) their fitness consequences on plants (Okubo and Levin 2001). In general, this inadequacy can be attributed to lack of data on the higher scales of quantification of dispersal patterns (Nathan and Muller-Landau 2000; Tackenberg 2003). Also, most of the reproductive biological studies are traditionally restricted up to the outcome of pollination studies and have not been effectively linked with dispersal. Therefore, the foundation of information on the dynamics of seed dispersal patterns is largely consolidated by ecological studies. These studies are focussed on the functional aspects of population growth, successional trends, resilience, reactions and community organization. This reliance on functional traits has retained its relevance even in current approaches as well. It has been emphasized that by considering the plant functional groups as analytical units of dispersal, it would be possible to distinguish and predict the components of the seed dispersal process of a focal species (Aslan et al. 2019).

As fruits and/or seeds are also the source of nutrition for animals, the dispersal mechanisms have evolved to escape predation and ensure the survival of a sizeable portion of the seed lot (Howe and Miriti 2004). The net recruitment in the community then eventually depends on the chances of occupying the ecological safe sites (*seed dispersal effectiveness, SDE*) available in the dispersal range of viable seeds (Wenny 2001; Schupp et al. 2010). Thus, the processes that contribute to the mortality of seeds during dispersal (*dispersal costs*) are *selected against dispersal* (Cody and Overton 1996; Clobert et al. 2001). The processes *selected for dispersal* may include kin competition and environmental heterogeneity (Auffret et al. 2017).

Like the pollination mutualism, dispersal mutualism is also generalized where more than one functional group of disperser may be linked to a plant species (Bascompte and Jordano 2007). With the involvement of different dispersers, variation in seed dispersal and recruitment pattern may arise due to the differential

assemblages and ability of the animals to remove seed crop across the distributional range of a plant species (Blendinger 2017). In anemochorous species (e.g. *Acer*), besides the morphological adaptations, settling velocity, height of release, wind speed and turbulence contribute to the pattern. The pattern is usually leptokurtic with majority of seed dropping close to the source, and the frequency recedes with distance (Okubo and Levin 1989).

1.8 Scope of Plant Reproductive Ecology

Reproductive processes, as briefly discussed above, play a crucial role in governing the adaptability of plants to multivariate environment. Knowledge of these key processes can prove useful in providing useful inputs in addressing the present-day challenges, which directly or indirectly impact ecosystem functioning. Incidentally, most of the challenges have emerged from direct human interference. Anthropogenic factors such as habitat destruction, over-exploitation and extreme modifications in land-use patterns have downsized the natural populations of many plant species. By elucidating the reproductive strategies of plant species, it is possible to predict their survival capacity and to take appropriate measures for their conservation (Bernardello et al. 2001).

In the current scenario, conservation and sustainable utilization of germplasm have become the priority of the species-rich regions. Most of these regions are located in the tropics, where forests have high endemism (Kier et al. 2009), and are also the major source of fuel, fodder, timber and alternative medicines (Bawa et al. 2004). The identification of the key reproductive requirements and constraints of threatened plants can help in species recovery (Kwak and Bekker 2006). For example, in *Sterculia urens*, besides the pollination constraint in fruit set, poor seed germination in nature and a longer seedling establishment phase (2–3 years) in the forests of Central India have been identified as the main reproductive constraints in the recruitment phase of the species (Sunnichan and Shivanna 1998; Sunnichan et al. 2004). For conservation of trees with obligate SI and those that exhibit strong inbreeding depression, maintenance of heterogeneous population of conspecifics is essential for the reproductive success and sustained recruitment process (Elam et al. 2007; Jones and Comita 2008; Singh et al. 2018). *Spilanthes acmella*, an important medicinal plant, is an over-exploited species, and its propagation by seeds is also limited because of the heterozygous nature of plants due to protandry that prevents self-pollination. In vitro methods can be employed to recover threatened plant species, as it has been done in *Eremostachys superba* (Sunnichan and Shivanna 1998). The species has mainly declined due to habitat destruction. For reintroduction, it has been recommended that populations should be supplemented with plants from distant populations to maintain heterogeneity (Verma et al. 2007). The problem of failed seed germination may be overcome by giving them pre-treatments or making artificial seeds. Therefore, for recovery of endangered species, combining the in situ or ex situ conservation approach along with those which reclaim habitats could be a useful strategy.

Akin to phenological changes, pollen-pistil interaction has been found to be sensitive to rise in temperature (Zinn et al. 2010). Elevated temperature has been shown to adversely affect pollen germination (Flores-Rentería et al. 2018). Likewise, many plants of medicinal and economic relevance have low fecundity due to abnormalities in pollen meiosis such as *Seasamum indicum* (Kumar and Yadav 2012) and threatened Himalayan poppy (Singhal and Kumar 2008). *Tetracentron sinense*, an economically important endangered tree species, shows the restricted distribution and poor natural regeneration due to abnormalities in the process of anther dehiscence, tapetum degeneration and pollen grain maturation (Gan et al. 2012). In *Coptis teeta*, an endangered medicinally important Himalayan plant, poor pollen fertility has been found to be the major impediment in sexual reproduction of the species (Pandit and Babu 1998). In smaller populations, the unavailability of sufficient viable pollen leads to an imbalance in sex ratio which effects population build-up and increases the probabilities of extinction (Frankel et al. 1995). Lower pollen viability, germinability and abnormal pollen tube growth have been attributed to reduced fruit set and sparse population distribution in *Rauwolfia hookeri* in the Western Ghats (Ranjusha et al. 2013).

Loss of habitats to expand urban development and modification in the land-use patterns for the cultivation of cash crops are the major issues faced in some tropical regions. Many of the crops cannot sustain prolonged storage (e.g. oil palm, sugarcane) and have to be processed within a short period of time to meet the commercial demand. Therefore, the processing units are also established along with the plantations. The immediate impact is seen in fragmentation of forests to smaller patches and consequent loss in the resilience of natural populations to recuperate. Disruption in the foraging range of pollinators due to fragmentation of a continuous habitat into smaller patches is the main reason for the drop in pollinator frequency in small populations. Moreover, such small populations with scattered individuals also fail to attract pollinators. Selective cutting causes microclimatic changes and decreases the amount of old and dead trees, which may threaten the persistence of many threatened species (Pykala 2007). Effects of genetic stochasticity such as inbreeding depression in small and fragmented populations of threatened plant species are also due to altered patterns of mating strategies and pollinator behaviour. In *Impatiens coelotropis*, a medicinally important and critically endangered species of South Western Ghats, reproductive stress is attributed to scattered and fragmented population distribution (Sreekala et al. 2008).

For recovering the forest corridors, rescuing dominant species to a viable population size can ensure a gradual build-up of the community and help in the re-establishment of key ecological associations. For example, mangroves are unique formations that regulate the ecosystem dynamics of coastal deltaic regions of the tropics (Upadhyay et al. 2002). These areas are also facing the vagaries of agricultural expansion. In such systems, true vivipary (seed germination when attached to the canopy of the parent plant) in some trees plays a crucial role in the recruitment process and regulates the dynamics of the entire ecosystem, while other species occur as associates (Solomon Raju 2013). Thus, by protecting the regenerative capacity of viviparous species in the forests, the mangrove ecosystem can be made