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REVIEW ARTICLE

## Loss of reproductive connectivity paves the way of plant species to red list status

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### Abstract

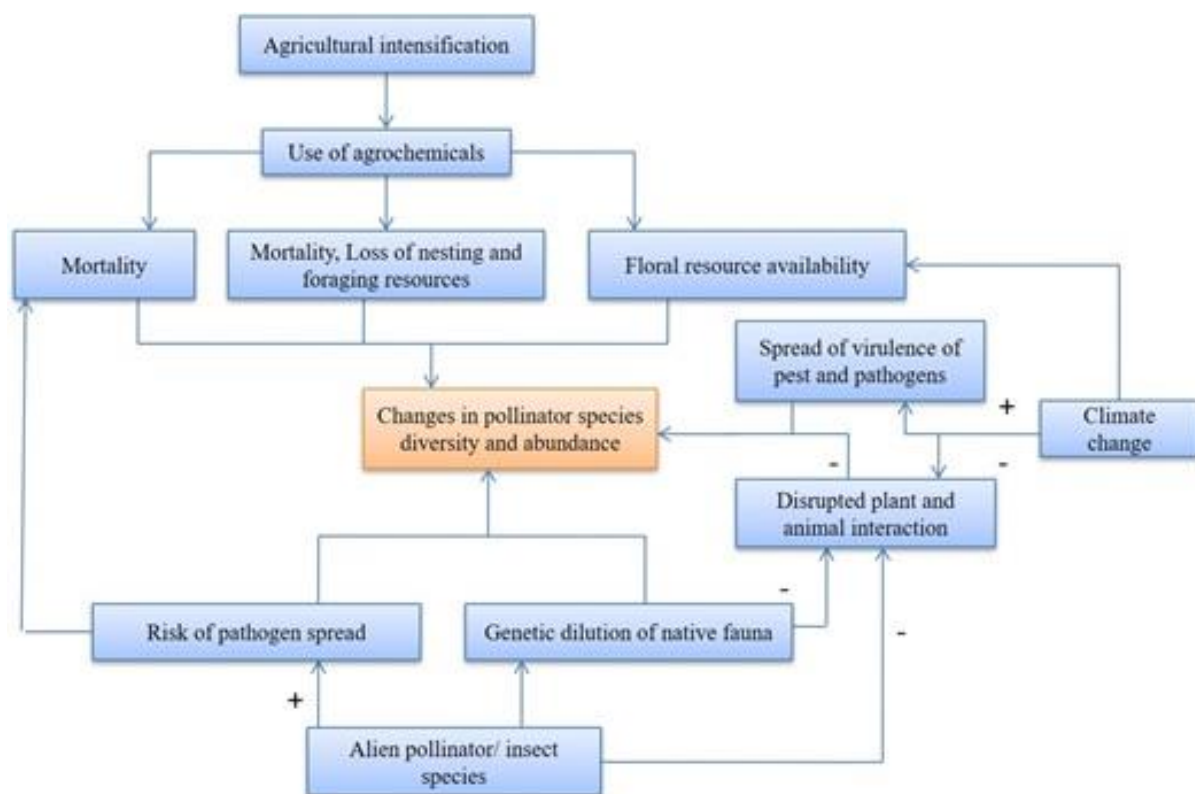
*The urge to produce progeny and perpetuate is inherent in all species. This instinct of a plant population gets threatened due to population bottlenecks and a reduction in genetic variability among the available mates. Gaining basic pollination and dispersal information is a critical step for understanding the geographical distribution of the species and for predicting the likely impacts of future climate change. Pollination and dispersal attributes, which plant species have adapted over time for favoring a particular type of pollination and dispersal strategy, lead to the co-evolution of species or the establishment of mutualistic interactions. These interactions are dwindling and pose threats to the conservation and reproductive connectivity of populations which proposes the first reason for understanding the advantage of seed dispersal for different endemic, endangered, and threatened taxa.*

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### INTRODUCTION

Effective reproductive success in the form of an optimal seed set and efficient recruitment of new individuals is imperative for the sustenance of a population. The reproductive fecundity of an individual and a population depends not only on the environmental conditions but also on the vegetative and reproductive growth of flora and the activities of pollinators and disperser agents. Regeneration of a plant species and preservation of the variation among the individuals in a viable population can be achieved only if all these processes are reserved in integrity. Reproductive potential holds a special relevance in biodiversity conservation which

when disrupted can negatively influence the cryptic survival of a species. There is no danger to the survival of the species if the rate of regeneration is more than the rate of species mortality or exploitation. As this condition gets reversed the threat perception develops. This may be in the form of non-availability of mates in dioecious and self-incompatible taxa or imposed by factors such as habitat loss, fragmentation, forest encroachment, etc. Plant-pollinator and plant-disperser relationships are among the most essential biotic interactions known in nature. Both these systems represent coevolved relationships of mutual benefit between plants and animals. This involves the dissemination of pollen or dispersals by pollinators and disperser agents (PDA) and in return provision of some incentives in the form of pollen, nectar, shelter, or fleshy fruit by plant to the former (Wheelwright and Orians 1982). Reproductive constraints lead to more mortality than births in the population which gradually decreases in size. Thus, ineffective reproduction and recruitment because of ongoing aforesaid causes is the ultimate reason for species vulnerability and eventual disappearance (Figure 1).



**Figure 1: Flowchart showing relationship between plant-pollinator/disperser and various factors affecting their interaction**

### Plant- Pollinator Relationships

Plant-pollinator interactions play a key role in maintaining the structure of terrestrial ecosystems. Globally, more than 87.5% of flowering plants are biotically pollinated (Ollerton 2011). In addition, 85% of the leading food crops are dependent upon biotic vectors for fruit-set. Biotic pollinators usually range from insects, reptiles, birds, and mammals to fishes and others that routinely transport pollen. Honey bees are alone reported to carry out seed-set of

>80% of the plants. In tropical forests, 98-99% of all flowering plants and 97.5% of all tree species rely on biotic vectors for siring their seeds (Bawa et al. 1985). In the temperate zone, 78% of the species are animal-pollinated. Pollination serves humans through the direct yield of crops (Klein et al. 2007; Ricketts et al. 2008) and indirectly through the maintenance of unmanaged ecosystems. Economically, these interactions have positive implications on crop productivity and food security. However, little is known about the effect of environmental disturbances on temporal and spatial variation in these interactions.

### **Importance of relationship**

Plants and pollinators are mutually dependent on each other. Loss in any of the components will hamper the survival of others. Recently, a considerable number of reports available from the USA, UK, Britain, and Netherlands have supported this. These reports have suggested that there is a substantial parallel decline in the number and diversity of both wild and cultivated insect pollinators (*Apis mellifera*, *Bombus* spp.) and plants relying on them (Biesmeijer et al. 2006). Similar speculations have been done for the “functional extinction” of birds and their dependent plant species in the northern islands of New Zealand (Anderson et al. 2011). In this way, pollinator decline leads to community-level changes through “species sorting” which involves the removal of pollinator-dependent plants (Pauw and Bond 2011). In the Indian context, several plant species are self-compatible, but to ensure better seed set through cross-pollination wait for the arrival of the pollinators. After a while, only due to the non-availability of the pollinators they accomplish seed-set through self-pollination by movement of style and stamens to gain proximity to each other (Philbrick 1984). Over time the populations of these species have reduced because of genetic bottlenecks and uniform genetic make-up the species is facing inbreeding depression and even low or complete absence of seed-set.

### **Plant-Disperser Relationships**

After pollination, seed dispersal is one of the major driving forces that is shaping the structure and dynamics of entire plant and animal communities. It is a non-passive process by which diaspores are dispersed away from the parent plant using intrinsic explosive mechanisms (ballistic) or by biotic and abiotic agents. Anemochory is common in the Alps and high mountains and is represented by 60% trees in the Alps and 20-25% plants in temperate rain forests of New Zealand. Myrmecochory is shown by 9% of flowering plants having small-sized dispersules and the presence of lipid-rich and proteinaceous elaiosomes. Mammalochory is prominent in 51-98% of the flowering plants. Interestingly, 90% of the plants in tropical rainforests represent endozoochory. However, only <5% of the flowering plants show epizoochory. Ornithochory is evident in 70% of the plants in tropical rain forests of New Zealand, 59% of plants in Amazonia, and 46-80% of plants in the Paleotropics. In the case of biotically dispersed species for ensuring effective seed dispersal, attracting a disperser agent is essential (Bollen et al. 2004). Thus, evolution has supported the selection of those characters which help in luring one kind of disperser agent more as compared to the other. The evolution of a high degree of reciprocal reliance and morphological or behavioral

specialization is also assumed to be present in certain seed dispersal systems (Howe and Primack 1975).

### **Importance of relationship**

Dispersal mechanisms can highlight important biological interactions between plants and disperser agents and are indicative of short- or long-dispersal events (Thomson et al. 2011) which are necessary for persistence, migration (Ozinga et al. 2009) and diversification of species (Ricklefs and Renner 2000). This process represents the initial template from which any regeneration starts however, with time demographic processes may entirely change the original spatial distribution pattern of plant recruitment. It has a profound effect on gene flow, ongoing interaction networks, and maintenance of biodiversity, in response to local climate change, invasions, and consequences of habitat fragmentation (Bascompte and Jordano 2007; Buckley et al. 2006). Seed dispersal away from the parent plant ensures increased survival of seedlings due to, encounters with favorable microsites, escape from density-dependent mortality near the parent plant, and competition with siblings due to similar nutritional requirements (Wright 1983). Moreover, due to a particular type of resource requirement and its abundant availability some pathogens, pre- or post-dispersal seed predators, parasites, and herbivores are primarily concentrated in areas where the density of a particular plant species is higher (Janzen 1970).

### **REASONS FOR THE POLLINATION NETWORK COLLAPSE**

Plant and pollinator/disperser density, their community composition, and ongoing interactions have been potentially altered by habitat modification/fragmentation including deforestation, land use changes, grazing by livestock, and forest/anthropogenic fires (Goulson et al. 2008; Hendrickx et al. 2007); overexploitation (Nunez-Iturri and Howe 2007); species invasions (Thomson 2006; Stout and Morales 2009); spread of pathogens (Neumann and Carreck 2010); climate change (Memmott et al. 2004); increased insecticide and pesticide usage and pollution. However, the interactive, or additive effect of one or more factors may severe the consequence of ongoing disturbance as seen in the case of honey bee colony losses in Australia, Fiji, and the Democratic Republic of Congo (Neumann and Carreck 2010). Managed *Apis mellifera* colonies in the US are also facing an acute reduction in their number owing to disease, misuse of pesticides, loss of governmental subsidies, and invasion of Africanized honey bees (Kremen et al. 2002).

### **Habitat modification and reproductive success**

Fragmentation and deforestation of habitat can detrimentally influence plant reproductive fitness (Aguilar et al. 2006) with a profound effect on pollination and dispersal systems. Small populations are more expected to accumulate incidences of inbreeding depression (van Treuren et al. 1991), genetic drift (Buza et al. 2000), mutualism disruptions (Agren 1996), and weed invasions (Morgan 1998). Isolation of populations owing to fragmentation can lead to disrupted interactions because of a reduction in overall relative diversity and abundance of pollinator and disperser agents. Fragmentation restricts the effective mobility of these agents

across several fragments (Murcia 1996). This reduced mobility may impose a negative impact in terms of decreased frequency of pollinator visitation to flowers (Kunin 1997) or changes in their behavior, pollen load, and pollen quality limitation on stigmatic surface culminating into low seed set (Jennersten 1988; Ghazoul and McLeish 2001). Changes in pollinator diversity and behaviour can also alter pollen donor and receptor relatedness leading to loss of genetic variability. Seedlings, thus, will have compromised fitness because of either inbreeding or outbreeding depression as seen in *Acer saccharum* and *Gentiana pneumonanthe* (Oostermeijer et al. 1994). In small forest fragments of *Astrocaryum mexicanum* an increase in accrual of non-pollinators as compared to pollinator species has been observed (Aguirre et al. 2011). It poses a threat to the pollination system of the plant due to increased competition between visitors and pollinators. Similar effects were also observed in the main and satellite islands of Ogasawara, where the mixing of visitor fauna with native fauna has potentially disturbed native pollination networks (Abe 2006). Conversely, some of the pollinator species such as Euglossine, tropical bees, and butterflies were found to be resilient to increasing landscape fragmentation (Powell and Powell 1987; Roubik 2001). Altered pollinator abundance and diversity in forest edges and highly fragmented areas cause changes in plant-pollinator interactions. This reduces plant density, causes local extinction, and shifts in tree assemblage as compared to forest interiors and as a result, brings reproductive impairment in biotically-pollinated plants (Aguilar et al. 2006). Studies carried out on pollinator abundance and diversity in Atlantic forests have documented reduced diversity of nectarivorous bats and hawk moths in smaller fragments. Severe reduction in functional diversity promotes the collapse of pollinator populations, restricts the ecological range of plant and animal groups, and alters the natural regeneration dynamics of forest communities in terms of species richness (Girão et al. 2007).

### **Reduction in functional diversity**

Functional diversity, exemplified by the presence of a variety of life history traits in a population assemblage (Fontaine et al. 2006), is important for maintaining ecosystem functioning (Tilman et al. 1997). Long-term outcomes of fragmentation and reproductive shift in terms of reduction in pollination systems, floral types, and floral sizes can lead to a reduction in the assemblage and functional diversity of a forest community. Changes in reproductive traits and functional diversity are derived from the proliferation of pioneer species and the decline in the population size of animal pollinators which alters original tree abundance. The proliferation of pioneer species is due to the predominance of their seed rain (Melo et al. 2006) and seedling assemblage in the soil. Oliveira et al. (2004) have reported an increase in pioneer species up to 80% of all the tree species in Brazilian Atlantic forests as compared to 50% in core undisturbed areas. On a broader scale this can strongly influence forest dynamics and pose a threat to biodiversity (Girão et al. 2007).

### **Climate change and disruption of networks**

Climate change also leads to altered interaction of plants and pollinators due to advancement or delays in flower production and interlinked visitation of pollinators (Wall et al. 2003). These changes directly threaten the reproductive connectivity of plants growing in a wide



geographical range. However, pollination networks are astonishingly nested and asymmetrical (Memmott et al. 2004) which involves the visitation of generalized pollinators to specialized plants and vice versa. Thus, in some way, specialists can be protected from immediate co-extinction, in the absence or loss of their partner (Aizen et al. 2009). However, these robust networks may also collapse in case of the severity of disturbances (Memmott et al. 2004; Fortuna and Bascompte 2006).

### **Consequences of reduction in Pollinator Diversity, Plant-Pollinator Interaction**

Fragmented habitats support less pollinator diversity as compared to undisturbed areas due to reduced food sources and nesting site availability (Harris and Johnson 2004; Cane 2001). The holometabolous life cycle of pollinator species which involves reliance on different resources from different habitats during different life stages, further adds to the complexity (Cane and Tepedino 2001). Fragmentation causes pollinator limitation due to low pollinator visitation in small, isolated, and low-density populations (Evans et al. 2003). Studies have documented a depressed abundance of nectarivorous bats (Sá-Neto 2003) and hawkmoths in small fragments (Lopes et al. 2006). In Britain and the Netherlands, scientists have reported a parallel decline in the number of insect-pollinated species and their pollinators and a comparative increase in wind-pollinated species. Proofs are also evident for the loss of *Bombus* sp. all over Belgium and the UK (Goulson et al. 2008; Biesmeijer et al. 2006). Pollen limitation because of scarcity of mates and pollinator guild loss, or compounded by both is a major factor likely to shape the evolution of plant reproductive strategies. The negative influence of a fragmented population is more evident where plants are in mutualistic interaction with pollinators, in the absence of which their reproductive success is affected. A reduction in effective population size decreases floral displays which fail to attract enough pollinators. Suppressed pollinator visitation decreases the number of pollen grains deposited on the stigma and results in a low seed set as observed in *Dianthus deltoideus* (Jennersten 1988). Nonetheless, the effects of population size reduction and low pollinator visitation rate can be buffered in those remnants where the pollinator guild is maintained by the density of flowering conspecifics. As evident in bumblebee-pollinated *Gentiana pneumonanthe* which shows a positive correlation of seed set with the number of flowering conspecifics in the area (Oostermeijer et al. 1998). Reduced reproductive fecundity and seedling establishment owing to pollen limitation because of scarcity of mates has been observed in several species such as *Banksia goodii*, *Primula veris*, and *Gentiana lutea* (Lamont et al. 1993; Kéry et al. 2000). A decline in population size causes a disproportionate reduction in population viability (Allee 1949). Although, seeds are produced in smaller populations as soon as the population reaches a critical size no seed production occurs (Lamont et al. 1993). Pollinator decline due to fragmentation may further worsen the effect of continuing pollen limitation in natural populations (Knight et al. 2005). Boyle and Menges (2001), have reported that insect visitation is density-dependent in *Hypericum cumulicola*, and seed set increases with an increase in population size. To achieve reproductive success, at this contemporary time, Thomann et al. (2013) hypothesized that plants can evolve in two different directions: (1) evolution towards less dependence on pollinators, and (2) evolution towards more resilient interaction with pollinators. According to the former, traits promoting high autogamy i.e.,

low herkogamy and dichogamy, shorter flower longevity, and lower pollen: ovule ratios are likely to be selected more as a part of adaptive evolution. During pollen limitation, due to lower pollinator density, selfing will somehow secure reproductive assurance up to a certain level, as a high selfing rate would lead to inbreeding depression. Thus, selfing traits which promote ovule siring by out-cross pollen first, is more advantageous as evident in *Ruta graveolens* and *Holcoglossum amesianum* (Ren and Tang 2012; Liu et al. 2006). This evolution is more beneficial for plants relying on specialists. In the second pathway, increased pollinator attraction strategies will help in coping with the decline in pollinator numbers especially for those plants that rely on generalist pollinators. Greater investment in male fitness to attract pollinators, as compared to female counterparts is more beneficial as high pollinator movement ensures pollen export when most of the ovules have already been fertilized (Vamosi and Otto 2002). In some plant species, an adjustment of flowering time with the availability of pollinators has also been found to be helpful (Devaux and Lande 2010). Higher autogamy for attaining reproductive success has been observed in *Centaurium erythraea* (Brys and Jacquemyn 2012). However, enhanced pollinator attraction in *Alkanna orientalis* supports the second scenario of evolution (Gilbert et al. 1996).

## REASONS FOR SEED DISPERSAL NETWORK FAILURE

### Habitat modification

In terms of fragmentation, intensive agriculture, and long-term grazing this is the chief cause for the threatened status of plant and animal biodiversity. These alterations not only disturb complex and above-ground species-rich biomass but also destroy seed banks that serve as an archetype for future regeneration and re-vegetation (Howe and Miriti 2004). Fragmentation and degradation of forests have led to the threatened status of the lion, *Leontopithecus rosalia* in the coastal Atlantic forests of Rio de Janeiro (Lapenta and Procopio-de-Oliveira 2008). Temporally, potential changes in plant-animal interactions, composition, and abundance can lead to reduced population size and/ or local extinction of the plant species (Wilcock and Neiland 2002). The introduction of exotic plant and animal species significantly affects the distribution of native species as well as alters ecological and evolutionary plant-animal mutualistic interactions. Disruption of mutualistic interactions can set plant partners on the road to extinction. In the Balearic Islands, the introduction of carnivorous mammals has led to the complete extinction of a lizard, *Podarcis lilfordi*. Lack of seed dispersal owing to the loss of its sole disperser agent shrub, *Daphne rodriguezii* is facing a low seedling recruitment rate (Traveset and Riera 2005). Human activities like harvesting fruits for consumption (Moegenburg and Levey 2002), excessive hunting (Wright and Duber 2001), or habitat modification (Cordeiro and Howe 2001), can lead to the disruption of mutualistic interactions and may predispose already endemic and endangered taxa to extinction. Cordeiro and Howe (2003) have shown a reduction in the number of disperser agents, seed removal, and seedling recruitment in the case of *Leptonychia usambarensis* due to the disintegration of the Tanzanian rainforest. Cramer et al. (2007) further added that since movements of large disperser agents are more altered as compared to small disperser agents large-seeded plants are more susceptible to extinction. Forest fragmentation can lead to a reduction in bird

species and failure in the recruitment of those plants that depend on them for germination. Fragmented landscapes can lead to loss or reduced abundance of some species and thus increase the rate of competition between dispersers and predators (Corderio et al. 2009). Density compensation between rodents (predators) and dispersers (birds) can enhance the predation of undispersed seeds. Moreover, if key disperser agents are very low in number or absent, a reduction in dispersal rate is obvious. Corderio and Howe (2003), Corderio et al. (2009) and Gorchoy et al. (1993) have observed much-reduced bird visitation in fragmented landscapes of African and Amazonian areas respectively, and found reduced bird-assisted dispersal in fragmented landscapes. Since, sparse, or low-density fruiting plants are less attractive to disperser agents.

### **Anthropogenic disturbances**

Disperser agents are critical to maintaining ecological processes in the forest ecosystem (Stevenson et al. 2005). However, excessive hunting of mammalian seed dispersers in tropical and Afrotropical forests is driving them to local extinction which is creating negative consequences for plants they disperse. Hunting pressure on tropical forests is rapidly increasing due to the increasing human population, accessibility to forests, and demand for wild meat (Robinson and Bennett 2004), fur, and bone. Repercussions of forest fragmentation and continued hunting on the dispersers and the plants have led to the extermination of animals ranging from small agoutis, monkeys, toucans, agoutis, peccaries, deer, and guans to large tapirs in the American tropics (Howe and Miriti 2004) which helps to disseminate seeds of various plants. A study conducted by Corderio and Howe (2003) reported a rare occurrence or complete loss of understory birds in fragmented patches that eat fruits of an endemic tree *Leptonychia usambarensis* in continuous rain forests Uriarte et al. (2011) showed reduced long-distance seed dispersal of *Heliconia acuminata* due to reduced density of its disperser bird, *Turdus albicollis*. Thus, plants growing in fragmented landscapes or undersized patches often face disperser limitations and constraints in regeneration. Genetic maternity exclusion analysis carried out by Wang et al. (2007) provides strong evidence for the above-mentioned fact as only 2% of *Antrocaryon klaineianum* endocarps found beneath the source plant were dispersed diaspores. The low dispersal rate and disruption in the seed dispersal cycle have been attributed to the loss of arboreal frugivores such as chimpanzees and gorillas.

### **Species invasion**

The introduction of exotic species and the spread of invasive species pose one of the major threats to the survival of native plant and animal species. Both, invasive plant, and animal species can change plant community composition. Extinction of browsing animals causes an increase in several seedlings on the forest floor and a decrease in their diversity. In forests where the extinction of dispersal agents occurs, the distribution of the same plants in disturbed and undisturbed patches is different. In southern California, invasion, and replacement of native ant *Pogonomyrmex* spp. by *Linepithema humile* have caused a noticeable drop in the seedling number of poppy trees *Dendromecon rigida* (Carney et al. 2003) owing to behavioral differences between the two species. These ants have also replaced



native seed-dispersing ants of South African shrublands resulting in dramatic changes in the plant community structure and a decrease in the density of large seeded plants. A better understanding of these complex systems is needed to conserve ongoing ecologically important relationships. A study carried out in north-eastern Georgia, demonstrates the effect of forest edges and red fire ant, *Solenopsis invicta* invasion on seed dispersal destination and distance on survival of bloodroot, *Sanguinaria canadensis*. *S. invicta* is the most common seed collector but a poorer disperser than most native ants. They frequently rob off seeds of their elaiosome and do not fulfill any of the dispersal conditions usually provided by native ants (Ness 2004). Lack of dispersal agents can negatively influence the genetic variability of a population due to the availability of genetic bottlenecks (Smouse and Sork 2004).

### **Reduction in seed disperser agent and its consequences**

The activity of frugivores has lots of benefits for the fruit or seed disperser agents and enhances seedling survival rate by transporting them away from density-dependent mortality near parent plants to special microsites (Howe and Smallwood 1982). In the Indian Eastern Himalayas, depauperate disperser assemblages have led to dispersal failure of seedlings of *Chisocheton paniculatus* from high mortality sites near adult fruiting trees (Sethi and Howe 2009). Thus, the extinction of disperser agents may lead to increased proximity of germinated seedlings to parent plants and a higher rate of damage from natural enemies (Hansen et al. 2008). Dispersal loss reshapes the entire forest community due to changes in the recruitment patterns of seedlings and juveniles. Sethi and Howe (2009) have reported dispersal limitation and a 77-69% decline in seedlings and juveniles attributable to hunting of hornbills by tribal communities. Commercial hunting of primates in otherwise undisturbed areas in Amazonian forests has caused inadequate dispersal and high mortality of recruits. According to Silva and Tabarelli (2000), 33.9% of tree species in the Brazilian Atlantic Forest, might be recruitment limited due to loss of its effective disperser agents. This reduced recruitment might lead to a gradual population decline. The absence of disperser agents due to hunting and other biotic factors affects seed and seedling recruitment rates as well as their predators (Roldan and Simonetti 2001; Galetti et al. 2006). In Central America where hunting has removed large rodents and seed disperser agents (Beckman and Muller-Landau 2007), predators serve the purpose of seed disperser and carry out effective seedling recruitment. Due to reliance on a few potential birds with wide gap widths for their dispersal, large-seeded trees have been expected to be more vulnerable and disperser limited in case of disperser loss (Wheelright 1985). Dunn et al. (2009) further added that increased specialization in plant and animal interaction will encounter severe consequences, as the extinction of one would lead to a knock-out effect on another. On the contrary, Moore and Swihart (2007) and Sethi and Howe (2008) proposed that apparent role redundancy among disperser agents might help some tree, which is visited by many frugivore assemblages, to overcome the loss of their main disperser agent. Primates (Christina et al. 2000), lizards (Traveset et al. 2012), bats (Duncan and Chapman 1999), and birds (Duncan and Chapman 1999; Neilan et al. 2006) due to their ability to disperse seeds act as a critical link between undegraded and degraded forests. These agents play an important role in the passive regeneration of degraded forests. However, in the Guam Islands, the invasion of a brown tree snake, *Boiga irregularis* has caused functional

loss of all the native vertebrate avian frugivores which resulted in a complete loss of seed dispersal service on this island (Caves et al. 2013). The wide distribution of the world's most sterile and asexually reproducing invasive species such as *Salvinia molesta* (Cilliers 1991) is an attribute of an effective seed dispersal mechanism. However, some species might become infertile due to rarity because of the absence of an effective disperser agent (Pilgrim et al. 2004). *Grevillea infecunda* is reported to never produce seeds owing to its restricted distribution (Kimpton et al. 2002). Species can become partially infertile and reproduce only asexually as evident in *G. althoferorum* (Burne et al. 2003) and *G. rhizomatosa* (Caddy and Goss 2006), respectively. Prolonged reliance on asexual means of regeneration affects the capability of sexual reproduction because of altered within- and between-population genetic structure (Honnay et al. 2006). Decreased sexual reproduction can threaten plants with extinction since it reduces the plant's adaptability to altered environmental conditions (Andersson 1994).

### **Impaired gene flow and reduction in genetic diversity**

Gene flow is the exchange of genetic information between populations either through the movement of pollen and/ or seed. The availability of large plant populations (Sork and Smouse 2006) and the undisturbed movement of pollinator/disperser agents are the two prerequisites for the maintenance of gene flow. From a conservation point of view, gene flow enhances out-crossing rates and has a strong influence on genetic drift and inbreeding (Ellstrand and Elam 1993). This movement is essential for upholding the connectivity and genetic diversity between populations and meta-populations of a particular plant species. Fragmentation of natural populations leads to decreased gene flow among the populations and reduces the genetic variation within populations due to genetic drift (Hartl and Clark 1997). This increases the local extinction of the population due to the formation of genetic bottlenecks. Thus, genetic variability is necessary to maintain the evolutionary plasticity of the species population as additive effects of reduced gene flow and fragmentation are going to be deleterious in the long run (Frankham et al. 2002). It has been observed that the tree species usually have high genetic diversity and their propagules flow to long distances, this feature makes them more resilient to fragmentation (Hamrick 2004). However, the survival and perpetuation of small and isolated populations with low genetic diversity is still a question (Young and Clarke 2000). The genetic diversity of a species relies on the fact of how distant its pollen flows and the diversity in the source of pollen and seed. However, due to underlying inbreeding depression high pollen flow does not always result in a high rate of pollen germination and fruit production (Nason and Hamrick 1997). Interestingly, those species that are pollinated by specialized pollinators are usually not affected by pollen flow (Nason et al. 1996). It is because the specialized pollinators such as wasps pollinating *Ficus* spp. can move in between small fragments of the population to find its conspecific mate even if it is quite far away (Nason and Hamrick 1997). Still, a high rate of movement amongst populations does not ensure protection for the population against reaching a genetic bottleneck and inbreeding depression.

### **Clustering of similar genotypes and Allee effect**

Persistent reduction in population size, due to genetic drift, lowers allelic diversity and frequency of cross-compatible mating systems (Reinartz and Les 1994). Thus, with time, even in the absence of connectivity through pollen and seed, the individuals of two meta-populations might genetically diverge in their mating patterns. In wind-pollinated and wind-dispersed tree species, there is a genetic similarity and clustering of related genotypes due to restricted pollen and seed flow (Epperson 1992; Epperson and Chung 2001; Seltmann et al. 2009). This can cause the effective extinction of the plants due to the presence of the same mating types or by hampering the seed set (Agren 1996; DeMauro 1993). In some species, the remaining populations are no longer fertile despite the availability of pollinators.

### **Inbreeding depression in condensed populations**

Decrease in the number of individuals of a population and resulting reduction in gene flow cause selfing or increase in mating among close relatives. This leads to the accumulation of biparental and uniparental inbreeding depression (Young et al. 1996). Individuals with a high level of inbreeding depression produce low-quality pollen grains that affect fertilization and reduce seed set (Johannsson et al. 1998). Less vigorous pollen grains also enhance the chances of fruit and seed abortion leading to a significant decrease in seed production (Hauser and Siegismund 2000). Lower pollinator visitation rates and deposition of lower quality pollen grains lead to inbreeding depression in *Calothammus quadrifidus* and *Ipomopsis aggregata* indicated by lower brood size and seed mass, respectively (Kunin 1997; Wilcock and Neiland 2002).

## **CONCLUSIONS**

On the global scale, an evaluation of the actual severity of the threat is a prerequisite for proposing and predicting suitable agri-environmental schemes for its mitigation. Ecologists need to pursue vigorous research work for precise future prediction of the effects of recent and projected environmental changes on ongoing pollination and seed dispersal networks. This will also help in assessing the viability of populations, phenological behavior of tree species, and flexibility of pollinator and disperser agent(s). Some bioeconomic assessments of the dependence of crops on pollinators and dispersers as well as the loss generated when these networks are lost have been done in some of the countries. However, due to worldwide heterogeneity in crop production, local abundance of insects, and ongoing land management policies (Gallai et al. 2009) a continental and regional evaluation is required. As a result of these concerns various continental, national, and regional initiatives have been launched such as the International Pollinators Initiative by Fifth Conference of Parties (CoP5) to the Convention on Biological Diversity in San Paulo Declaration (1999), International Initiative for the Conservation and Sustainable Use of Pollinators (IICSUP 2000) and recent launch of All India-Coordinated Research Projects (AICRP) on Reproductive Biology of 40 Rare, Endangered and Threatened Tree Species (2010-14) by Ministry of Environment, Forests & Climate Change (MoEF&CC), New Delhi, India. Conservation of rare, endangered, and threatened plant species along with maintenance and recovery of viable populations, habitat

restoration of mined areas, and continuation of genetic variability among species populations should be the eventual endeavor. Ongoing conservation practices should aim at stopping the further isolation of different fragments. This can be achieved by maintaining a continuous pollen-mediated gene flow between fragments and the creation of buffer zones in already fragmented populations (Richards 2000; Tewksbury et al. 2002). This allows easy movement of pollinators and dispersers along the fragmented landscapes. Furthermore, any protected area does not behave as an isolated island from the border environment and most of the biodiversity grows outside these protected areas also. Thus, adapting the “off-reserve management” policy will help in the conservation of species along with their associates which ensures the evolution of viable populations. To combat the problem of inbreeding depression, genetic heterogeneity in the species can be promoted by manually cross-pollinating the flowers with pollen obtained from plants located at different sites (Das 2015). Pollinator limitation not only affects a particular species, but it also affects a complex array of networks. The loss of pollinators and disperser agents threatens their services to both wild and crop plants. Conservation of pollinators and dispersers through increased availability of nesting and breeding sites could be one of the alternatives. Population structure studies show that insect pollinators like bumblebees cannot be conserved in minute secluded areas but require larger suitable habitats to sustain long-term viable populations. Thus, integrating large field areas will be more advantageous as compared to the localized efforts. Additionally, attracting birds and their loads of seeds through placing perches and planting a variety of shrubs and trees in the field can lessen the disadvantages caused by habitat modification. This helps in achieving a dispersal pattern that promotes re-vegetation. The provision of government subsidies for employing Agri-environment schemes and environmental assessment of pesticide toxicity prior to release will be helpful in the restoration of threatened pollinator and disperser species. Despite all the reported regional losses, there has been a 45% increase in worldwide bee hives. However, this increase is not effective since the number of crops dependent upon these pollinators has increased many a fold [ $>300\%$ ].

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