PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Do Mutualisms Matter? Assessing the Impact of Pollinator and Disperser Disruption on Plant Extinction

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Phil. Trans. R. Soc. Lond. B 1994 **344**, 83-90
doi: 10.1098/rstb.1994.0055

Do mutualisms matter? Assessing the impact of pollinator and disperser disruption on plant extinction

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SUMMARY

There is a voluminous literature on pollination and dispersal, very little of which deals with the consequences of reproductive failure and its most extreme consequence: extinction. The risk of plant extinctions can be assessed by considering the probability of dispersal or pollinator failure, reproductive dependence on the mutualism and demographic dependence on seeds. Traits for ranking species rapidly according to these three criteria are indicated. Analysis of case studies suggests that plants often compensate for high risk in one of the three categories by low risk in another. For example, self-incompatible plants with rare specialist pollinators often propagate vegetatively. Some systems, including elements of the Cape flora and lowland tropical rain forest, lack compensatory traits and the risk of plant extinction from failed mutualism is high.

'What escapes the eye, however, is a much more insidious kind of extinction: the extinction of ecological interactions' Janzen (1974).

1. INTRODUCTION

Ecology has contributed two major insights to the biology of extinction: large areas hold more species than smaller areas and larger populations persist longer than smaller ones. No comparable generalization has emerged from studies of ecological interactions. In this contribution I attempt a new approach to predicting extinction which explicitly includes the importance of interactions. The patterns that emerge are not used to make general statements on probable species loss but rather to identify general traits which increase extinction risk. I use the interaction between plants and their pollinators and dispersers as an example of this species-centred view. These reproductive mutualisms epitomize the subtle, complex web of interactions which, if broken by human actions, could cause a cascade of extinctions (Janzen 1974, 1987; Kevan 1975; Vogel & Westerkamp 1991; Gess & Gess 1991).

To address the question of whether a wave of plant extinctions will follow the collapse of pollinator and dispersal interactions, and to help avert them, I ask: (i) Which traits indicate vulnerability?; and (ii) Which species are threatened and in what systems? There is an enormous literature on pollination and a growing literature on dispersal (see, for example, Boucher 1985; Estrada & Fleming 1986), very little of which is informative for predicting extinction (although see Gilbert 1980; Howe 1984; Addicott 1986). The biology of reproductive mutualism is notoriously complex (Boucher 1985; Howe & Westerley 1988). To make the problem of predicting extinctions manageable, I focus on ecological rather than genetic or evolutionary consequences and ecological time scales of centuries rather than evolutionary scales of millennia.

2. THREATS TO POLLINATORS AND DISPERSERS AND PLANT RESPONSES

Pollinators and dispersers, both vertebrate and invertebrate, face diverse threats. These include poisoning by pesticides (Johannsen 1977; Kevan 1975; Kevan *et al.* 1985), habitat alteration (Janzen 1987; Gess & Gess 1991), invasions of alien animals and plants (Bond & Slingsby 1984; Breytenbach 1986) and insularization of habitats (Linhart & Feinsinger 1980; Diamond 1984; Jennersten 1993). There seems little doubt that the community of pollinators and dispersers is being altered by these and other forces. The consequences are likely to be a reduction in diversity of animal mutualists, and changes in population densities of the survivors. It is tempting to argue that specialists dependent on a few species will be more vulnerable than generalists. However, the diversity of threats is so great that whole assemblages of mutualists may be eliminated. No mutualism is completely assured.

The pathway to extinction is not a simple one for plants deprived of their mutualist partners. Key considerations are: (i) the probability of a mutualism failing; (ii) the degree of reproductive dependence on mutualism (facultative or obligate); and (iii) the importance of seeds in the demography of the plant. All are important in assessing extinction risk. For example, inclement weather often disrupts pollinating insects in temperate and alpine habitats. However, many herbaceous plants in these habitats are self pollinated or have such a diverse pollinator fauna that

Phil. Trans. R. Soc. Lond. B (1994) **344**, 83–90
Printed in Great Britain

seed set is assured. A few with specialist pollinators may fail to set seed but persist by vegetative propagation. These compensatory mechanisms – self pollination, flowers pollinated by a generalist fauna, or escape from demographic dependence on seeds – may ensure persistence in many habitats where pollinator services are unreliable. Similar considerations apply to dispersal mutualisms. Each of the contributing factors can be evaluated on a scale indicating increasing vulnerability to provide simple qualitative criteria for assessing risk. Far more complex approaches are needed for fully quantitative analyses of particular populations (see Price & Jenkins 1986).

3. THE PROBABILITY OF MUTUALISMS FAILING

Both the likelihood of a particular mutualist being lost and the possibility of its reproductive services being replaced need consideration. Most plants are pollinated by several to many species, often of widely diverse taxonomic origin (see, for example, Feinsinger 1983, 1987; Janzen 1983; Schemske 1983; Herrera 1984; Herrera 1988). Pollination by a single species seems to be very rare though figs, *Yucca* and orchids include notable exceptions. If field studies are lacking, pollinator specificity may be crudely assessed from floral morphology. Increasing specialization is associated with traits that limit pollinator access including complex shapes, large size, long corolla tubes, and floral orientation (Faegri & van der Pijl 1979; Linhart & Feinsinger 1980; Motten 1986) or specialized attractants and rewards (Dafni et al 1990; Johnson & Bond 1993; Steiner 1989). Dafni (1992) provides a useful practical guide to pollination biology. Increasing specificity of dispersal agents is associated with increasing fruit or seed size for birds (Martin 1985; Herrera 1984; Wheelwright 1985) and some mammal faunas (Janzen 1986; Janzen & Martin 1982). Similar trends have been reported for Australian ant-dispersed species where large seeds with large rewards are more likely to be carried by non-destructive ants (Hughes & Westoby 1992).

Using these criteria or others derived from field knowledge, the probability of pollinator or disperser failure for a plant species can be ranked as illustrated in table 1. I have used an arbitrary scale from 0 (wind or abiotic) to 1 (single species dependence). Plants with several mutualist species may still be vulnerable if these are all closely related.

4. REPRODUCTIVE DEPENDENCE ON MUTUALISM

The degree of dependence on mutualism for reproductive services varies greatly. The breeding system of a plant is of major importance in assessing its dependence on pollinators. This may vary from none in asexual and self-pollinated species to facultative in self-compatible species and obligate in self-incompatible and dioecious plants (Richards 1986). Rapid surveys of breeding systems can be made from herbarium material (e.g. Cruden 1977; Plitmann & Levin 1990) but should preferably be supplemented by hand-pollination studies in the field (e.g. Bawa *et al.* 1985; Dafni 1992). The frequency of asexual seed production may be underestimated by these simple methods (see, for example, Ha *et al.* (1988) for tropical forest trees). Breeding systems can be ranked on a scale from 0 to 1 to indicate relative dependence on pollination for seed set (table 1).

The dependence on dispersal for seedling recruitment is far less well understood but it appears to vary just as much with some species highly dependent on dispersers for germination (see, for example, Janzen (1983) for a review) or recruitment (e.g. Augspurger 1984; Beattie 1985; Slingsby & Bond 1985; Louda 1989) and others not (e.g. Janzen 1983; Pierce & Cowling 1992). But, in principle, dispersal dependence too can be ranked on a scale of 0 to 1 indicating increasing dependence on the process for recruitment (table 1).

5. DEMOGRAPHIC DEPENDENCE ON SEEDS

Reproductive mutualisms are a favourite subject for the study of adaptation using seed set or seedling recruitment as measures of fitness. However, evolu-

Table 1. *Plant attributes and extinction risk*

(Extinction risk is greatest when the risk of pollinator/dispersal failure, reproductive dependence on the process and demographic dependence on seeds are all high. *PS* = pollinator, *DS* = disperser specificity, *BS* = breeding system, *DD* = dispersal dependence, *SD* = population dependence on seeds.)

		dependence on process		
rank	risk of process failure (*PS*, *DS*)	pollination (*BS*)	dispersal (*DD*)	dependence on seeds (*SD*)
high 1	single species dependence	dioecious self incompatible	dispersal obligatory to cue germination, reach safe sites, evade predators	seed propagation only, lifespan (10^0–10^2 years), killed by disturbance, few large seeds, no seedbank, sparse seedlings
	specialist	self compatible		
	generalist			
low 0	wind	self pollinated apomicts	dispersal not needed for germination, recruitment or survival	vegetative propagation, lifespan (10^2–10^4 years), resprouts after disturbance, many small seeds, persistent seed bank, dense seedlings

tionary importance is not synonymous with ecological importance. The frequency of a trait may change under selection without altering the size of the population (Addicott 1986). The distinction between ecological and evolutionary importance has seldom been recognized in studies of mutualism but is central to predicting extinctions. Pollinator or disperser failure will only affect extinction when populations are seed limited.

An important measure of relative dependence on seeds is the number of generations needed to persist for some given timespan, say 200–300 years. Traits associated with low risk then include: (i) clonal or vegetative propagation (Richards 1986); (ii) long lifespans; some plants persist for thousands of years (Loehle 1988; Pigott 1993; Tredici 1992 for Ginkgo); and (iii) the capacity to resprout vegetatively after disturbance such as fire or hurricanes. Plants with shorter generation times may still have low dependence on seeds if seedling densities greatly exceed the space available for adults (Harper 1977; Anderson 1989; Crawley 1990). Thus seed predators are usually poor agents for biological control of weeds because high levels of seed predation achieve little more than the removal of suppressed individuals (Wilson 1964; Harper 1977; Hoffman & Moran 1991).

Some populations, however, are strongly influenced by seed predators. Examples include annual herbs (Borchert & Jain 1978; Anderson 1989), shrubs (Louda 1982), especially fire-prone non-sprouting species (Bond 1984; Bond & Slingsby 1984; Cowling *et al.* 1987), mangroves (Smith 1987) and fugitive species from ephemeral habitats (Louda 1989).

Demographic dependence on seeds can be ranked on the basis of these considerations (table 1). The least dependent are those species that, once established, persist indefinitely by clonal propagation or vegetative sprouting. This is one of the easiest traits to identify in the field or from herbarium material or taxonomic monographs. The most seed-dependent species have sparse populations producing few seeds that are short lived, lack seed banks and are killed by disturbance.

Compensatory effects

These three factors, the specificity and degree of reproductive dependence on mutualism, and the demographic dependence on seeds, may compensate to reduce the risk of extinction. A study of spring wildflowers in temperate deciduous forests serves as an example (Motten 1986). This community should be highly susceptible to pollinator failure because of the high diversity of insect-pollinated species, the short blooming season before canopy closure and poor weather that interrupts pollinator activity. This is not the case as shown by plotting species location on axes of dependence on pollinators against demographic dependence on seeds (figure 1). Species with the highest demographic dependence on seeds cluster at the low risk end of the pollinator dependence axis: they are all self pollinated or have diverse bee and fly pollinators. At the opposite extreme, species with high pollinator dependence cluster at the low risk end of the seed dependence axis: they are clonal and very long lived. No species occupies the most vulnerable area in the top right corner.

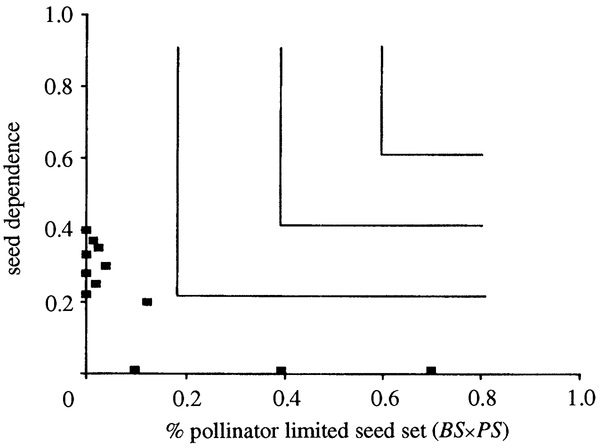

Figure 1. Reproductive compensation in spring-flowering herbs of a temperate deciduous forest (Motten 1986). Pollinator-limited seed set ($BS \times PS$) is plotted against demographic dependence on seeds from clonal = 0 to short lived, sparse = 1. Contours indicate increasing risk of extinction from the origin.

Similar patterns occur in Welsh populations of *Veronica* species (Boutin & Harper 1991). The short-lived seed-dependent species are self pollinated or self compatible whereas potentially pollinator-limited species are clonal and long lived (table 2). Extreme examples of pollinator limited seed set occur in some long-lived clonal species. *Filipendula rubra*, a rare self-incompatible North American herb, has very low seed set in nature (less than one viable seed per thousand ovules) but, like other clonal species, genets may be hundreds or even thousands of years old (Aspinwall & Christian 1992).

The frequency of compensatory mechanisms suggests extinction may have already removed high risk specialists. Alternatively, self pollination may have evolved rapidly in response to pollinator failure (Motten 1986) or selection may have altered floral morphs to allow visits by alternative pollinators.

Table 2. *Compensatory effects in the genus* Veronica *growing in Britain*

(Short-lived species have breeding systems or pollination modes which ensure seed set. Self-incompatible species with large, presumably more specialized pollinators are clonal and therefore insured against reproductive failure (Boutin & Harper 1991). BS = breeding system, PS = pollinator specificity, SD = seed dependence, $BS \times PS \times SD$ = extinction risk.)

species	BS	PS	$BS \times PS$	SD	$BS \times PS \times SD$
arvensis	0.1	—	< 0.1	annual (1)	*ca.* 0
hederifolia	0	—	0	annual (1)	0
persica	0.1	—	< 0.1	annual (1)	*ca.* 0
serpyllifolia	0.5	0.2	0.1	clonal (0)	0
chamaedrys	1	0.5	0.5	clonal (0)	0
filiformis	1	0.5	0.5	clonal (0)	0

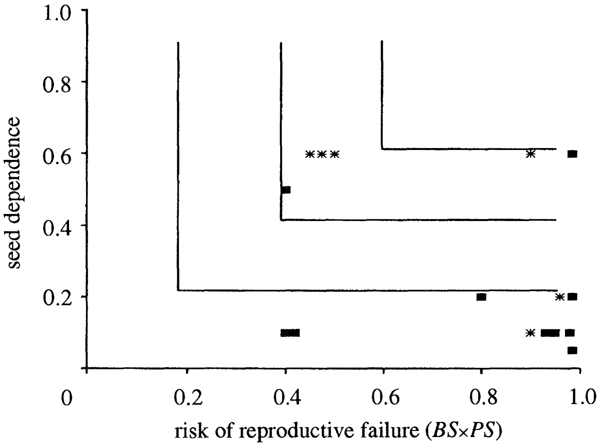

Figure 2. Compensatory effects in a guild of species all pollinated by a single butterfly species, *Meneris tulbaghiae*, in Cape fynbos (see Johnson & Bond 1993). Endangered species are marked with asterisks. Contours indicate increasing risk of extinction from the origin.

Compensation is not universal. A single species of butterfly is the near exclusive pollinator of a guild of 15 spectacular red-flowered species from four families (Iridaceae, Orchidaceae, Amaryllidaceae, Crassulaceae) and seven genera in the fynbos vegetation of South Africa (Johnson & Bond 1992, 1993). Most of the species are incapable of selfing and seed set often fails (Johnson 1992). Demographic dependence on seeds is poorly known for this largely geophytic guild. Most of the streambank species are capable of vegetative propagation. The bulbs of amaryllids are probably longer lived (e.g. Snijman 1992) than irid corms (J. Vlok, unpublished data). The orchids produce hundreds of tiny seeds from a single capsule and may be site rather than seed limited (Calvo 1993). Figure 2 ordinates the species, on the basis of available information, on axes of reproductive dependence on the butterfly versus demographic dependence on seeds. Unlike the temperate herb flora, nearly half of the butterfly guild has no compensatory mechanism for surviving pollinator failure. This may have caused the extreme rarity of a large proportion of the species (figure 2). Alternatively the syndrome may have evolved because the butterfly is a reliable pollinator of sparse populations (Johnson 1992).

Compensatory mechanisms in dispersal are much more difficult to identify. They imply that species with obligatory dependence on dispersal persist because they have reliable (generalist?) dispersers or are not seed limited.

6. A VULNERABILITY INDEX FOR POPULATION CONSEQUENCES OF MUTUALISM

The three concerns, risk of pollinator or disperser failure, reproductive dependence on the mutualism and demographic dependence on seeds, can be combined in a subjective index for rapid assessment of extinction risk. A simple formula which caters for compensatory effects by taking products is:

$$VI=[(BS\times PS)+(DD\times DS)]\times[SD].$$

Here VI is a vulnerability index, BS stands for breeding system, PS for pollinator specificity, DD for disperser dependence, DS for disperser specificity and SD for demographic dependence on seeds. The first term in square brackets on the right hand side refers to reproductive effects, and the second to demographic effects. Species are ranked for each class using the criteria listed in table 1. For example, a self-pollinated, wind-dispersed annual has a $VI=[0\times y+z\times 0]\times[1]=0$, where y and z may be unknown but there is obviously no population consequences of failed mutualism. In contrast, a rare, butterfly-pollinated, short-lived *Gladiolus* may have a $VI=[1\times 1+y\times 0]\times[1]=\geqslant 1$, and the species is flagged as vulnerable. Note that partial information is adequate and that any value approaching 1 implies vulnerability. The index is useful both as a heuristic tool for thinking about the population consequences of mutualism or as a practical way of quickly assessing vulnerable species.

It is possible to use either pollination or dispersal information or both depending on completeness of information. Breeding systems and pollinator and disperser specificity can be derived from field information or herbaria records when these are not available using the criteria listed in table 1. Consideration of seed dependence is essential if there is concern for imminent extinction. Some indication can be gleaned from herbaria or systematic monographs, such as sprouting capacity, clonal propagation or seed size, but field observations of criteria listed in table 1 would be more valuable.

7. CASE STUDIES

The risk of extinctions due to collapse of mutualisms varies greatly among taxa and region. In highly seasonal climates, most plants seem well insured against pollinator failures. Wind pollination, self pollination and asexual propagation are common at high latitudes and altitudes (Richards 1986; Regal 1982). Entomophilous flowers in temperate areas often have very diverse pollinator faunas and are well buffered against pollinator failure (Schemske 1983; Herrera 1988; Howe & Westerly 1988). The compensatory effects illustrated in figure 1 and table 2 may therefore be quite common.

(*a*) *Cape Proteaceae*

An interesting contrast is seen in the fire-prone shrublands of Australia and South Africa. Proteaceae are prominent in the extremely species-rich fynbos flora of the Cape. According to the vulnerability index, nearly 50% of the more than 300 species in the Cape flora are threatened with extinction should their mutualisms collapse. This is because the populations of many species appear to be strongly seed limited: most do not sprout after fire, seeds are few and large and seedling populations are sparse with little evidence for self thinning (Le Maitre & Midgley 1992). Despite this risky life style, most are well buffered against pollination failure. The dioecious genera are either wind pollinated or pollinated by numerous insects, especially beetles (Hattingh & Giliomee 1989). Many species of *Protea*, *Mimetes* and *Leucospermum* have large showy inflorescences pollinated by birds. However, exclusion experiments have shown that *Protea* species are also pollinated effectively by a variety of insects, especially beetles (Coetzee & Giliomee 1985; see also Vaughton (1992) for Australian *Banksia*).

Seed dispersal in fynbos Proteaceae is either by wind or ants. Experimental studies suggest that the ant dispersed species have a near obligate dependence on dispersal to escape rodent predation or fire (Bond & Slingsby 1984; Slingsby & Bond 1985). At least one ant-dispersed species behaves as a fugitive as parental sites are invaded by more competitive wind-dispersed species after fire (Yeaton & Bond 1991). A variety of ant species disperse seeds suggesting a low risk of dispersal failure. However, small parts of the region have been invaded by the Argentine ant, *Iridomyrmex humilis*, which displaces most native species. It does not disperse seeds into ant nests resulting in heavy seed losses and very poor seedling recruitment in invaded areas (Bond & Slingsby 1984). Should *Iridomyrmex* continue to spread, nearly half the fynbos Proteaceae may be lost.

This example clearly illustrates the dilemma in estimating extinction risk based only on dispersal specificity. One never knows which group of mutualists will be threatened nor how complete local extinction may be. In this case, the near obligate dependence on the mutualism and the demographic dependence on seeds are better indicators of vulnerability.

Fynbos is also rich in extraordinary and highly specific pollination mutualisms. Many of the most beautiful plants are pollinated by a sparse and unusual pollinator fauna of long tongued flies, oil collecting bees, monkey beetles, large carpenter bees and the butterfly *Meneris tulbaghiae* (Rebelo 1987; Johnson 1992; Steiner 1989; Manning & Linder 1992). These species seem particularly vulnerable to pollinator failure. However, information on pollinators, breeding systems and demographic dependence on seeds is too limited for any general assessment at this stage. In a recent analysis of threats facing the flora, not a single Red Data Book species was listed as threatened by extinction of its mutualist partner (Rebelo 1993). This probably says more about the cryptic nature of extinctions caused by failed mutualism than indicating the real magnitude of the problem.

(*b*) *Tropical rain forest*

Tropical forests may also be high risk floras. Lowland tropical forests in particular are marked by unusually low levels of self pollination and very high levels of dioecy (table 3; Bawa *et al.* 1985). In contrast to temperate regions, lowland tropical forests have much more specialized pollinator and disperser relationships (e.g. Regal 1982). Obligate one to one pollinator relationships (such as figs and fig wasps) are the exception in the tropics but most species are pollinated by only one or a few species belonging to the same taxonomic group (e.g. euglossines, hummingbirds, scarab beetles, bats, etc.) (Bawa 1990). The combination of self incompatibility and pollinator specificity indicates a high degree of reproductive dependence on mutualism.

Table 3. *Distribution of breeding systems (% of tree species) in tropical forest trees (ex Bawa 1990)*

forest type	self comp.	self incompat.	dioecious
TLRF, Costa Rica	20	80	23
montane forest, Venezuela	62	28	31
montane forest, Jamaica	85	15	21

The same may apply for dispersal. Neotropical rain forests have a very high proportion of fleshy fruits in canopy trees (Howe & Westerley 1988), less so in Asian and African forests, but all forests have a high incidence of fleshy fruits in the sub canopy. At least some studies suggest near obligate dependence on dispersal for recruitment so that reproductive dependence on mutualisms may also be high for dispersal (Howe & Westerley 1988; Augspurger 1984).

There is much less information on demographic dependence on seeds. Many tree populations are sparse with little density-dependent mortality (Hubbel & Foster 1990). Fugitive species (*Cecropia*) exploiting light gaps may be seed limited (Garwood 1989). Tropical trees are difficult to age and I have no information on the incidence of sprouting after disturbance. If sprouting is rare, then the cascade of extinctions envisaged by Janzen (1974, 1987) may be true for plants as well as their animal partners.

8. EXAMPLES OF POLLINATOR AND DISPERSER EXTINCTION

There are several convincing cases of complete extinction of animal partners in reproductive mutualisms but very few of subsequent plant extinctions. Janzen has argued persuasively for extinction of a guild of mammals that dispersed large fruits in the neotropics and arid lands of North America but the plant species still persist thousands of years after the loss of their dispersers (Janzen & Martin 1982; Janzen 1986). The oil-collecting bee pollinator of a rare fynbos shrub, *Ixianthes*, has become locally extinct but the plant sprouts and is not immediately threatened with extinction (Steiner 1993). Temple (1977) argued that recruitment of a Mauritian tree may have failed because its seeds needed processing by the extinct dodo. However, the tree still survives on Mauritius. In Hawaii, extinction of native bird pollinators resulted in a change of pollinators for the ieie, *Freycinetia arborea*, not extinction (Cox 1983). It is arguable whether the persistence of plant species for hundreds, if not thousands of years, after extinction of their mutualist partners is evidence for general resilience to extinction or just the tip of the iceberg of all the other species that went extinct.

9. CONCLUSIONS

This analysis of the importance of an ecological interaction for predicting extinction differs from previous ecological studies of extinction risk. It cannot make broad generalizations such as those offered by island biogeographic theory, nor explicit probabilities of extinction time such as population vulnerability analysis. However, it does identify species threatened by the extinction of interactions. The approach explicitly takes into account compensatory effects that may reduce the threat. Taxonomic databases can be useful for partial assessments of vulnerability but should be supplemented by field surveys. The point is that the approach is feasible: it can be included in surveys of extinction threats.

The longer view

I have taken a short-term view of the impact of animal extinctions on plant extinctions. The importance of interactions for species persistence has been ignored for too long. However, lists of threatened plant species are not the true measure of the problem for conservation. Few would disagree that the extinction of the interaction itself is of much greater concern. It will be tragic if the remaining natural areas of the world are filled with ageing plants silent as graveyards with no butterfly or sunbird pollinators working their flowers or large colourful birds eating their fruits.

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