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Reproductive ecology of *Cycas beddomei* Dyer (Cycadaceae), an endemic and critically endangered species of southern Eastern Ghats

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Cycas beddomei **is an endemic and critically endangered, tropical, dry deciduous, dioecious gymnosperm confined to India. Coning and leaf flushing events occur during April–June. The plant is typically anemophilous and it is highly effective for optimal seed set. In both the sexes, during maturation process the cones show weak thermogenesis and emit mild foetid odour, which apparently do not have any significant role in pollination.** ***Alphitobius*** **beetles use male cones for feeding and breeding during which they get coated with pollen. These beetles in search of other male cones visit female cones by mistake and effect pollination. The female cones offer only warmth to the beetles during night. The beetles diapause on male plants or in the soil until the next coning season. Leaf flushing episode occurs immediately after the maturation of cones in both sexes, to gain the lost energy and also to supply photosynthate for the growing seeds in female plants. The squirrels,** ***Funambulus palmarum*** **and** ***Ratufa indica*** **act as seed dispersal agents. A beetle species uses the seeds for breeding and causes seed infestation to a great extent. The adults that emerge from the seeds diapause in the soil until the next seed season to repeat the next breeding cycle. The study suggests that the restricted participation of plants in the annual coning event, restricted seed dispersal, seed infestation and other factors relating to natural regeneration contribute to the endemic and endangered status of the plant.**

Keywords: *Alphitobius* sp., anemophily, *Cycas beddomei*, leaf phenology, seed infestation.

LITTLE is known about the pollination systems and pollinators of the ancient group of cycads, as only a few have been studied[1]. Detailed pollination studies are available for only four of the world's eleven cycad genera. Hall *et al.*[2] reviewed the experimental studies of pollination in all cycads so far carried out by different workers and concluded that these cycads are primarily entomophilous: *Zamia furfuracea* by *Rhopalotria*, *Zamia pumila* by *Rhopalotria*, *Pharaxonotha*, *Encephalartos cycadifolius* by *Metacucujus*, *Encephalartos villosus* by *Parthetes*, *Macrozamia macdonnellii* by *Cycadothrips*, *Macrozamia communis* by *Tranes*, *Bowenia spectablis* by *Miltotranes* and *Lepidozamia peroffskyana* by *Tranes*. The family Cycadaceae represents a single genus *Cycas*, the sole living *Cycas* group occurring in Asia. It consists of about 100 species, out of which 40 are Indo-Chinese, 27 are Australian and the distribution of the remaining species has not been clearly documented. *Cycas* occurs in the Malaysian region, Japan, India and Sri Lanka, extending to Micronesia and Polynesia, Madagascar and East Africa[3]. In *Cycas*, pollination mechanisms have been discussed by different workers. In *Cycas circinalis*, the pollen is transferred to female cones by the wind, while pollen is transferred from female cones to ovules by both wind and water[4]. In *C. panzhihuaensis*, the first phase of pollen transfer from male to female cones occurs by wind, and the second phase from female cones to ovules by insects[5]. Wind is the major pollination agent in *C. seemanni*[6]. In *C. rumphii* and *C. thouarsii*, the strong odour and thermogenesis in male and female cones serve as a mechanism to attract insects for pollination[7]. Norstog

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and Nicholls[8] speculated that *C. media* is probably insect-pollinated. Kono and Tobe[9] showed that *C. revoluta* is primarily entomophilous. In India, eight species have been reported so far – *C. beddomei*, *C. circinalis*, *C. indica*, *C. sphaerica*, *C. annakailensis*, *C. nathorstii*, *C. pectinata* and *C. zeylanica*, with the first five species occurring only in India[3]. There is no information on the pollination ecology of any of these species. In this communication, we present the demography, coning phenology, agents of pollination and seed predation in *C. beddomei*, and these aspects are discussed in the light of existing pollination information on cycads.

C. beddomei is a critically endangered species with a population size less than 1000 trees extended in an area of 50 sq. km at an altitude of 650–1500 m. It is restricted to dry, open hill slopes, in the open grassy woodland or grassland of Seshachalam hills of Chittoor and Cuddapah districts, Andhra Pradesh, eastern India. In 1985, this species was listed in Appendix 1 (which prohibits trade in wild-collected plants, except for scientific or conservation purposes) of CITES[10,11]. Further, it was included in the list of specified plants according to the Schedule 6 of Indian Wildlife (Protection) Act 1972 (ref. 11).

Two populations of *C. beddomei*, one at Dharmagiri and another at Talakona, situated about 65 km apart from each other (GPS coordinates 13°40′N, 79°19′E and 3556 ft) in the Seshachalam hill range, Chittoor District, were selected for the study during 2008–2009. The Dharmagiri site with an area of 5 sq. km, is characterized by a combination of rocky, undulating and steep terrain with higher litter content formed from grass, silver oak trees and some herbaceous plants during summer season, with an average temperature of 33.1 ± 2.96°C (range 28–37°C) and average relative humidity of 42.4 ± 7.93% (range 31–55%). Grasses and herbs show luxuriant growth during the rainy season. On the contrary, the Talakona site is at the hilltop, with an area of 15 sq. km, characterized by open, near-flat surface with red soils covered by minimal litter content during the summer season. Dharmagiri site was selected for the study of all aspects detailed in this communication because at the other site, participation of female plants in annual coning event is poor.

Demographic studies were carried out with reference to total plants, and coned male and female plants during the study period; age aspect was not studied due to its low stem stature. Plant characteristics, and leaf and coning phenology at population level were carefully observed. Leaf characteristics and leaflet number per leaf were also recorded, for which five leaves each from five male and five female plants were taken. Demographic study was carried out at both the sites to determine the proportion of plants participating in the annual coning episode.

For all aspects of the present study, 10 male and 10 female plants were selected keeping in view the endangered status of the plant. Five representative young cones of each sex were selected and monitored over the duration of the pollination season to record the cone development sequence. The intact male and female cones were also examined for heat production during maturation period; the temperature level within and outside the cone before, during and after pollen shedding in the male cone and at different times during maturation of the female cone was measured using a thermometer. A horizontal cut was made up to the axis of the male cone and inserted thermometer to measure temperature. The early stage of female cone prior to ovule initiation was used to insert the thermometer into the base of the cone to measure the temperature. In five male cones, the arrangement and number of microsporophylls, and the number of sori consisting of microsporangia were recorded. The pollen grain characteristics, output per microsporangia/microsporophyll/cone, and pollen–ovule ratio were estimated following the protocol of Dafni *et al.*[12]. Pollen protein content per microsporophyll/cone was estimated according to the method prescribed by Lowry *et al.*[13].

The activities of the beetle were monitored on both male and female cones from the time of its arrival to the time of its departure. The beetle-life cycle stages on male cones were examined in detail. Further, its sensitivity to light was examined by disturbing some individuals manually within the cone. Five intact female cones were tagged and monitored at different time intervals to evaluate the role of the beetle in pollen transfer from male cones. Five female cones were used to record the number of megasporophylls/cone and the number of ovules/megasporophyll/cone. Ten ovules were used to record the characteristics of the ovule. Two female cones completely free from beetles were tagged, meshed and monitored to evaluate the role of wind in pollination and subsequent seed set. The pollen grain characteristics were examined for anemophilous traits. The site and plant characteristics with reference to air circulation were also considered to evaluate the efficiency of anemophily. An anemometer was used for noting wind direction. Ten intact female cones were used to record seed set in open pollination. The duration of seed growth and development was also observed by following ten female cones periodically until maturation. Ten intact female cones were selected to record seed characteristics. Observations were also made on seed dispersal agents and seed predators. A beetle species used the fallen seeds for its breeding. Two hundred fallen seeds were collected and examined for seed infestation rate by this beetle. Seed germination and seedling establishment were not found at the study sites and hence these events were not quantified. However, 50 seeds collected from Dharmagiri site were used to evaluate seed germination rate and this experiment was conducted in experimental plots at Andhra University.

C. beddomei is a small, palm-like shrub with an erect solitary stem up to 1.23 ± 0.18 m long (range = 1–1.6 m)

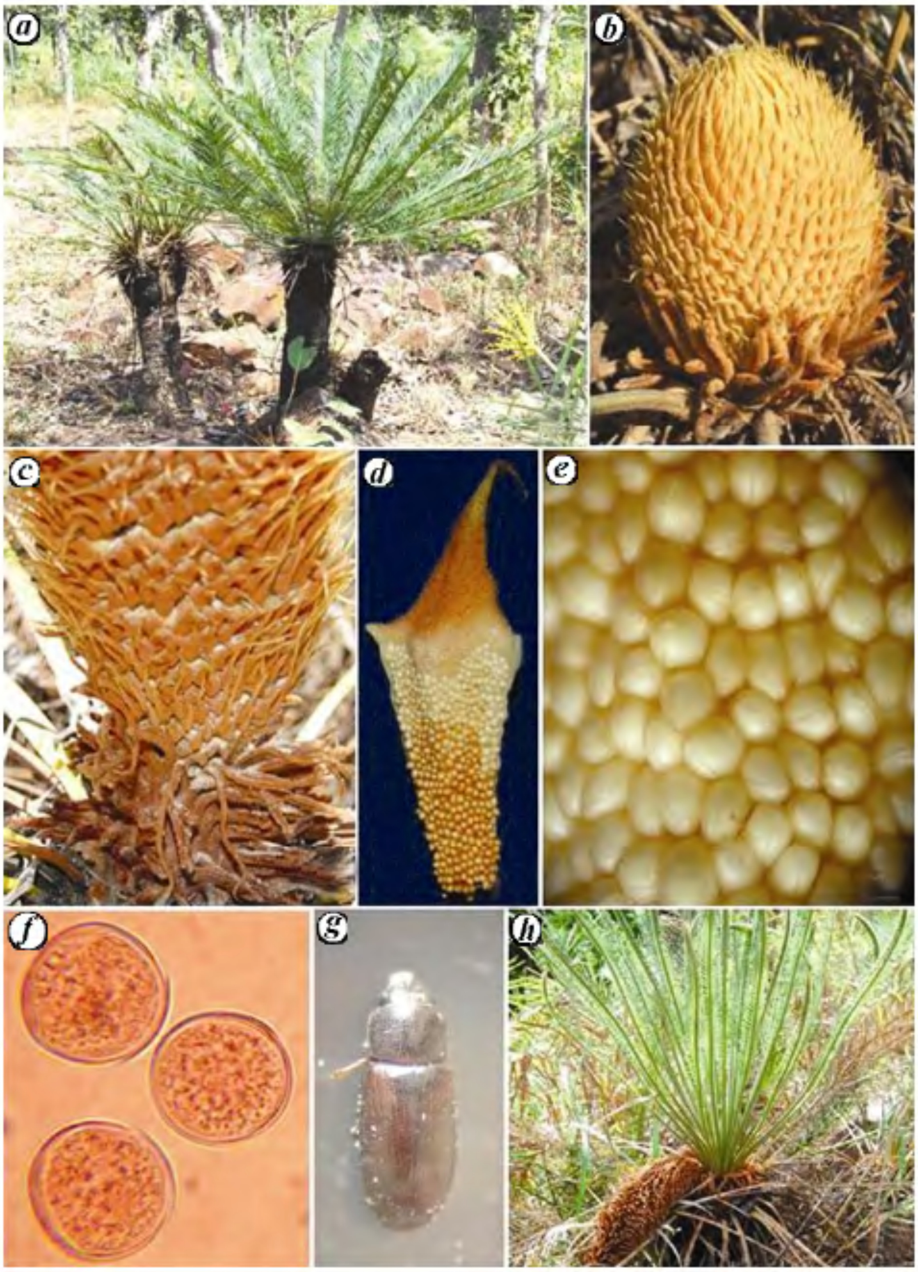

Figure 1. *Cycas beddomei*. ***a***, Short-stemmed plant with a crown of leaves at the top; ***b***, Male cone; ***c***, Male cone at pollen-shedding stage; ***d***, Abaxial surface of microsporophyll with sori; ***e***, Sori about to shed pollen; ***f***, Spheroidal, uniaperturate pollen grains; ***g***, *Alphitobius* beetle; ***h***, Leaf flushing following withering of male cone.

and often shorter diameter (15–20 cm). The top of the stem is crowned with 20–30 pinnately compound leaves (Figure 1 *a*). Vegetative propagation is absent. Seed is the only mode of propagation. It is dioecious, but sex detection is possible only during the coning phase. Coning male and female plants are leafless prior to the formation of cones. The male cones occur in different stages from the first week of April to the third week of June, whereas the female cones show different stages from the second week of April to the fourth week of June. Male and female plants produce a single cone at the top of the stem. The demography of the two populations examined at Dharmagiri and Talakona sites showed different patterns. At Dharmagiri, coning plants represented 64.9% of the population in 2008 and 19.4% in 2009; their sex ratio was 66% male in 2008 and 53.3% male in 2009. At Talakona, only one female cone was evidenced in both 2008 and 2009, whereas total absence of male cones was evidenced in 2008 and 17 male cones in 2009 (Table 1).

Male cones are short-stalked, compact, narrowly ovoid woody structures, orange in colour, 29.95 ± 3.98 cm long and 7.5 ± 5.78 cm diameter (Figure 1 *b*). A cone consists of 820 ± 131.3 microsporophylls which are arranged spirally around a central axis. All the microsporophylls are fertile, except a few at the basal and apical parts of the cone. Each microsporophyll is a woody, orange-brown, 3.98 ± 0.32 cm long, and more or less horizontally flattened structure with a narrow base and an expanded upper portion. The adaxial surface does not bear microsporangia, whereas the abaxial surface bears microsporangia up to the wedge-shaped expanded part of the microsporophyll (Figure 1 *d*). The microsporangia occur in groups of 3 or 4; each such group is called a 'sorus' (Figure 1 *e*). Each microsporophyll produces 453.8 ± 48.22 sori and each sorus produces 12,605 ± 1547.8 pollen grains. The pollen output per microsporophyll is 5,720,149 ± 702,409. Each male cone produces 4,690,529,980 ± 546,414,045 pollen grains. The pollen grains are light yellow, powdery, spheroidal, 24.6 ± 0.29 μm in size, uniaperturate, unicellular and uninucleate, surrounded by an outer thick exine and inner thin intine (Figure 1 *f*). The total protein content in all the microsporangia of a microsporophyll is 4.22 ± 0.16 mg and per cone is 3.45 ± 0.45 g.

Male cones produce heat at maturation during which the axis elongates, loosening the microsporophylls. Temperature increases slightly during elongation and pollen shedding. Just before pollen shedding, the temperature is 35.5 ± 1.27°C within the cone and 34.5 ± 1.87°C outside the cone. During pollen shedding, it is 37.4 ± 3.05°C within the cone and 34.1 ± 2.96°C outside the cone. After pollen shedding, it is 34.5 ± 1.72°C within the cone and 33.6 ± 1.74°C outside the cone (Figure 2). The temperature regime during the cone maturation process shows that endogenous heat production causes a rise of 3.3°C against the ambient temperature outside the cone during the pollen shedding process (Figure 1 *c*). At this stage the cone produces mild foetid odour, which could be detected at a distance of 1–2 m from the plant; the odour subsides at the end of pollen shedding. At this stage, the cones attract *Alphitobius* beetles (Coleoptera: Tenebrionidae) which upon arrival remain within the cone, and feed only on the parenchyma within the microsporophylls prior to mating (Figure 1 *g*). Female beetles deposit their eggs within the microsporophylls. The larvae emerging from the hatched eggs feed on the parenchyma and pupate within a week. The adults that emerge from the pupae move within the interior of the cone and in so doing get dusted with pollen. They then fly to other male cones in search of food and shelter, and also visit female cones. The beetles dusted with pollen occur in small numbers on cones of female plants and they may effect pollination. The beetles are sensitive to light and hence are active during dusk and early evening hours. Some beetles stay in the unexposed areas of the stem throughout the non-reproductive phase of the plant and become active during the next coning event.

Table 1. Demography of *Cycas beddomei* coning at the study area

	Dharmagiri site		Talakona site	
Plant aspect	2008	2009	2008	2009
Total plants	77	77	265	265
Total plants with cone*	50	15	1	18
Total male cones	33	8	0	17
Total female cones	17	7	1	1

*Each coned plant produced a single male/female cone only.

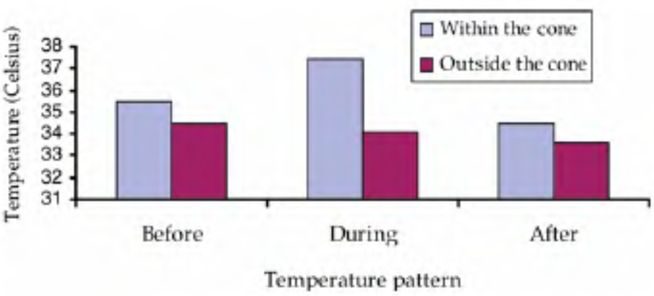

Figure 2. Temperature pattern during the course of pollen shedding in male cones of *C. beddomei*.

In male cones, the microsporangia of all microsporophylls commence dehiscence synchronously, but in each microsporophyll the dehiscence is gradual from the base to the top, and is indicated by the colour change of the microsporangia from creamy-white to brown. The pollen being powdery drops off and accumulates on the adaxial side of the microsporophylls which are situated below, and it is easily blown away into the atmosphere by the wind. The high wind conditions together with the low height of the stem, sloping terrain and scanty vegetation drive out the pollen effectively into the atmosphere, ensuring receipt of pollen by the ovules on the megasporophylls of female trees. In two female plants located about 60 m away from the coned male plants, the cones that were meshed prior to formation of ovules to exclude the visits of *Alphitobius* beetles, were found to set seed; it was 45% in one plant and 48% in another plant. This seed set was considered to be exclusively a function of wind-driven pollen prior to bagging of female cones. The male cones gradually withered and bent to one side, but remained on the male plant for about one year. The bent male cone makes way for the emergence of new leaves at the top of the stem (Figure 1 *h*). The male plants remain leafless without the formation of cones in the consecutive year.

Female plants produce megasporophylls that are not organized into cones; instead they occur in close spirals in acropetal succession at the apex of the stem (Figure 3 *a*). However, this reproductive structure is also called as 'cone'. Each cone consists of 42 ± 11 megasporophylls which are brown, tomentose and 17.92 ± 1.61 cm long. Each megasporophyll is differentiated into a basal stalk and an upper pinnate flat lamina which is lanceolate and

Figure 3. *C. beddomei*. ***a***, Female cone; ***b***, Growing seeds covered by megasporophylls; ***c***, Leaf flushing through the centre of female cone; ***d***, Exposed seeds; ***e***, Aborted ovules; ***f***, Four-seeded megasporophyll; ***g***, Manure seed; ***h***, Dry seeds; ***i***, Seed infestation by a beetle; ***j***, Close-up view of adult beetle seed predator.

strongly toothed with an acuminate spine that is quite distinct from the lateral spines. A megasporophyll bears 1–6 ovules on the lateral sides of the stalk; single-ovuled megasporophylls are 3%, two-ovuled 18%, three-ovuled 13%, four-ovuled 53%, five-ovuled 5% and six-ovuled 8%. The ovules are sessile, orthotropous, greenish-yellow, hairy, globose, unitegmic, 2.2–3 cm long and 1.8–2 cm diameter with a reddish-brown micropyle tip. The integument is three-layered with an outer fleshy layer (sarcotesta), middle stony layer (sclerotesta) and inner fleshy layer which remains in close association with the nucellus. Collectively, a cone produces 81 ± 32 ovules, out of which 44 ± 6 set seed in open pollination. Female cones produce weak foetid odour when mature, but the temperature within the cone and outside is almost the same. When fully developed the female cones expose the ovules slightly. The pollen dispersed by wind and/or beetle reaches the nucellar surface of the ovule; 37–165 pollen grains were found at the nucellar surface. The pollen thus germinates to produce a pollen tube which penetrates the nucellar region and subsequently delivers the male gametes into the archegonial chamber. The diploid zygote develops into an embryo. The fertilized ovules show slow development to form seeds, taking about one year for complete development into seeds. Aborted ovules shrink, turn reddish-brown and finally become black (Figure 3 *e*). The developing seeds bulge out gradually through the spaces between the megasporophylls (Figure 3 *b* and *d*). The new leaves emerge from the centre of the megasporophylls as soon as the ovules are fertilized, grow well during the rainy season and mature during late winter (Figure 3 *c*). The seeds are ovoid, 3.4–4.5 cm long, 3.3–3.4 cm wide, initially green, and yellow to orange when mature (Figure 3 *f* and *g*). The embryo is white, cellular and the upper region elongates into the suspensor. The outer surface of the integument eventually becomes wrinkled; at this stage seeds fall to the ground for dispersal (Figure 3 *h*). Three-striped Palm squirrel, *Funambulus palmarum* and Indian Giant Squirrel, *Ratufa indica* feed on the fleshy sarcotesta of the seeds, carry them to other places and hence act as seed-dispersal agents. The fallen seeds are dispersed by rainwater due to their floating ability. But, the rugged and stony terrain mostly blocks dispersal by rainwater. The decomposition of sarcotesta takes place naturally, exposing the same to enable seed germination. Seed germination experiments indicated that seeds are not dormant. They germinate readily if the soil is wet, and if soil is dry, seed mortality occurred. Seed germination rate is 35%. The seeds are vulnerable to predation by an unidentified beetle. This beetle gradually penetrates into the interior of the seed to feed on the inner fleshy endosperm and produces a single generation of offspring (Figure 3 *i* and *j*). The adults emerge from such seeds and move into the soil for diapausing until the next coning season. Seed infestation rate is 62.5%. No seed germination and seedling establishment was observed at the study sites.

Published reports on cycads do not provide any clue regarding leaf phenology. In the dioecious gymnosperm, *C. beddomei*, leaf flushing occurs following the event of pollen shedding in coned male plants and following the fertilization of ovules in coned female plants during April–June. The immediate leaf flushing activity in coned plants may help gain the lost energy in both sexes and also to supply the photosynthate for the growing seeds in female plants.

In cycads, determination of sex of a plant is possible only when the coning event occurs[14]. In *C. beddomei* also, sex identification is possible only in coned plants as non-reproductive characteristics do not give any clue for sex determination. Demography and cone production of *C. beddomei* for two consecutive years at the two study sites show that all plants do not participate in the annual coning event and the percentage of participating plants varies from year to year. At the Talakona site, coning in a single plant in the first year and in a few plants in the second year of study suggests that annual reproductive activity is restricted in this population. Restricted participation in the annual coning event and the coning of a few female plants in each year appear to be partly responsible for the limited population size. Such restricted participation in the annual coning event has been shown to be a typical feature of cycad populations, and this is possibly because of high resource cost associated with such massive reproductive structures[15–18]. Copious pollen production by male cones enables *C. beddomei* to achieve optimal seed set in coning female plants. Such a situation has also been reported in *Lepidozamia peroffskyana*[2].

Tang[19] reported that in cycads, male and female cones number from one to several per plant. But *C. beddomei* produces a single cone per plant in both sexes and hence the number of male and female cones is always equivalent to the number of coning male and female plants. Published reports indicate that *C. circinalis* is pollinated exclusively by wind[4]; *C. panzhihuaensis* and *C. seemanni* by wind and beetles; *C. rumphii*, *C. thouarsii* and *C. media* by beetles[7,8], and *C. revoluta* primarily by beetles. Thermogenesis and odour production occur during the process of maturation of male and female cones of *C. rumphii*, *C. thouarsii* and *C. revoluta*; the odour attracts beetles in both sexes and the beetles visiting the cones effect pollination[7]. In *C. beddomei*, heat and odour resulting from developmental and metabolic processes in both sexes are weak, especially so in female cones. The odour is not perceptible beyond 2 m radius. The beetle-exclusion experiment with two coned female plants demonstrated that optimal seed set occurs in the absence of beetle activity and anemophily is highly effective. All of these suggest that the plant is not adapted for entomophily.

Proctor *et al.*[20] stated that anemophilous species produce typically non-sticky pollen grains that disperse singly and easily. In the habitat of such species, every square metre must receive around a million pollen grains to make pollination reasonably certain. Hall *et al.*[2] reported that the pollen would be even higher in the habitat of anemophilous species since the micropyles of ovules are not exposed to the open air, but are sheltered behind a barrier of megasporophylls. In *C. beddomei*, the coning male plants produce trillions of light, dry and powdery pollen grains at the population level and disperse singly and easily into the air. The meteorological conditions for airborne pollen transport are optimal during the coning season of the plant. A close synchrony exists among the coning male and female plants, and this facilitates anemophily to be highly effective. These findings are in agreement with Faegri and van der Pijl[21], and Proctor *et al.*[20] who stated that genuinely wind-pollinated plants are characterized by mechanisms to ensure that the pollination phase is closely synchronized between individuals and that the pollination event is initiated when meteorological conditions for airborne pollen transport are optimal. Kono and Tobe[9], in their work on the pollination of *C. revoluta*, mentioned that wind is effective for pollination only when both males and females grow densely in windy, open areas. In this study, both the work sites are windy – the wind blows from the top to the bottom along the steep sloping terrain at Dharmagiri site, whereas it blows nearly uniformly in all directions at Talakona site. In Dharmagiri site, the male and female plants occur in small groups with each sex group consisting of 3–4 plants and a few male plants scattered singly. The spatial distribution of male and female plants at Talakona site is not known, as there was only a single coned female plant in each year during the two-year study period. The two study sites are open areas and characteristically dry deciduous with sparse vegetation during the coning season; this condition makes anemophily more effective. Therefore, *C. beddomei* is primarily anemophilous.

C. beddomei attracts *Alphitobius* beetles at the time of maturation of male and female cones. In male cones, the beetle feeds on the parenchymatous tissue of microsporophylls; the parenchyma has been reported to be rich in starch[22]. After feeding, it mates and produces a single generation of offspring within two weeks. The adults thus emerged carry pollen and in search of other maturing male cones they also visit female cones by mistake and hence effect pollination. The beetle is a short-distance flier and its flight activity takes place during dusk and early evening hours due to its sensitivity to bright sunlight. The area being windy, the wind may also drive the beetle to extend its flight activity, thus increasing the distance of pollen transported by it. The beetle attempts to collect food at the micropyle region of the ovules on the female cones, but this region does not have any fluid or fluid-like substances and such attempts result in pollen transfer to the micropyle from where pollen enters the archegonia. It does not breed on female cones, perhaps due to starch-poor megasporophyll tissue[22]. We see a small number of beetles on female cones, since the latter do not offer feeding and breeding environment. Therefore, visits of *Alphitobius* beetles account for additional pollinations only.

In *C. beddomei*, the beetle produces offspring on dry and dead rachis of male cones after pollen shedding. This shows that its presence does not cost the male plants in any way. The beetle seems to be attracted to both sexes of the plant due to similar colour of the cones, and in this process the pollen-covered beetles effect pollination accidentally on female cones. The beetles enjoy an ecological niche with this plant. The male cones offer protective colouration, shelter, warmth during night, feeding and breeding environment to the beetles, whereas the female cones offer protective colouration, shelter and warmth during night. Similar state of ecological niche offered to other beetle pollinators has been reported in *Zamia furfuracea*[22] and *Chamaerops humilis*[23]. In *C. beddomei*, the beetles visiting the female plants depart as the latter do not provide either food or breeding environment, whereas those visiting the male plants either fly to other male or female plants or remain in the unexposed areas throughout the non-reproductive phase of the plant, without any feeding and breeding. Such a state represents diapause, a type of dormancy or mechanism whereby some kind of adversity is circumvented, whether of climate, or of availability of food and/or oviposition sites. This arrested state of development throughout the non-reproductive phase of a specific host plant has been well documented[24,25]. The reproductive continuity of *Alphitobius* beetles from season to season is related to their survival during diapause on male plants of *C. beddomei*.

In cycads, almost all parts of the plant produce toxins, the concentration of which varies with each part. The seeds also contain toxins, usually have brightly coloured sarcotesta, and attract a variety of birds and mammals. These animals feed on the fleshy sarcotesta and disperse the seeds which are protected by a hard sclerotesta[26]. The sarcotesta is barely toxic, or if it does contain toxins, the animals that feed on this layer somehow cope with it, like many animals do with toxic angiosperm fruits[8,27]. The squirrels feed on the sarcotesta of *C. beddomei* and disperse the seeds with sclerotesta intact. Other animals such as rodents, bears and birds were also present in the study sites, but we never found them feeding on the seeds of *C. beddomei*. In the absence of information on the chemical nature of the seeds of *C. beddomei,* it is not reasonable to suggest why squirrels alone feed on the seeds. Rainwater also disperses the seeds, but the rugged terrain of the area does not permit dispersal far away from the parent sites. Charlton *et al.*[28], and Norstog and Nicholls[8] reported that in cycad seeds the endosperm and the embryo are well supplied with toxins for protection against herbivores. Despite the toxicity of the inner part of the *Zamia* seed, a specialized weevil uses it for its breeding[26]. In *C. beddomei*, an unidentified beetle raises a single generation of offspring in the interior of the seed and the emerging adults diapause in the soil until the next seed season. This beetle is responsible for a larger percentage of seed infestation or predation, and hence is regulates the reproductive success and population size. Seeds germinate readily if soil conditions are favourable, and if not they perish; this is evidenced in our experiments. Natural regeneration is lacking at the study sites. We assume that the grasses and other seasonal plants utilize the available nutrients in the soil and litter, overgrow and suppress the seedlings of *C. beddomei*, which have been found to grow slowly in the experimental plots.

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