Snail-pollination in *Volvulopsis nummularium*

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Pollination is a crucial ecological process that aids sexual reproduction in flowering plants. Although a variety of animals are known to bring about pollen transfer, pollination by snails (malacophily) has remained a rare and obscure phenomenon. Here we conclusively demonstrate the incidence of malacophily in *Volvulopsis nummularium* (family Convolvulaceae, commonly known as the morning glory family), a prostrate rainy-season weed, which is also visited by honey bees. Flowers open in the morning and last only for half a day. *Apis cerana indica* and Graceful Awlsnail (*Lamellaxis gracile*) are the pollinators. Snails are exclusive pollinators on rainy days, when bees are not active. Contrary to the belief that snails are destructive, we found that they do not affect the natural fecundity of *V. nummularium*. Manual-pollinations indicated that the plants were facultative autogamous. Pollination in *V. nummularium* by snails and honey bees represents an interesting guild, which is of adaptive significance in achieving high reproductive success without resorting to obligate selfing.

Keywords: Honey bees, malacophily, reproduction, snails, *Volvulopsis nummularium*.

POLLINATION is a significant process and one of the prerequisites for ensuring fruit- and seed-set in all sexually reproducing seed plants[1–3]. A great majority of plants are pollinated by animals[4] and only a few involve abiotic agencies[1,5–7]. Among the zoophilous species, nearly 80% are pollinated by insects. The remaining involve a variety of birds, reptiles and mammals[8–11]. Pollination by snails and slugs (malacophily) is a rare and infrequent phenomenon; so far it has been reported in seven species: *Rohdea japonica*, *Philodendron pinnatifidum*, *Colocasia odora*, *Calla palustris*, *Lemna minor*, *Chrysosplenium alternifolium* and *Phragmipedium caudatum*[12–14]. Prostrate habit of the plant and floral arrangement in which the stigma and anthers do not extend much beyond the corolla, are believed to be conducive to malacophily[12]. However, some investigators doubt the possibility of snails or slugs being successful pollinators, and consider malacophily to be 'notorious and obscure'[15] or even 'ridiculous'[14].

Snails are usually active at night and also during the day in the rainy season. In an unexpected field observation, we found mass floral foraging by the terrestrial garden snail – the Graceful Awlsnail (*Lamellaxis gracile*) on a common garden weed, *Volvulopsis nummularium*, in which flowers open in the morning and close by noon. This is a small (~15 mm in length) terrestrial snail commonly found throughout India and other tropical and subtropical parts of the world, except Australia[16]. We made a detailed investigation on the pollination ecology and breeding system of *V. nummularium* to ascertain whether (i) snails have a definite role in pollination, (ii) their exclusive foraging could induce fruit and seed-set and (iii) phytophagy by snails is destructive to the natural fecundity of this plant.

V. nummularium (L.) Roberty (syn. *Evolvulus nummularium* L., family Convolvulaceae), a native of tropical America, is a weed with prostrate and creeping habit that has naturalized in moist places in several parts of India[17]. The plants are multi-stemmed and propagate profusely through seeds as well as by vegetative means. Profuse growth of neighbouring individuals leads to the formation of expanded mats with overlapping stems. The plant becomes conspicuous when it starts blooming with the onset of monsoon (Figure 1 *a*). Peak flowering is reached by mid-August and lasts for a month. White, short tubular flowers are borne solitarily, and sometimes two in number, in the leaf axil. There is no previous report about any specific pollinator of *V. nummularium*.

A general survey of the distribution of plants of *V. nummularium* was carried out in Delhi region (28°12′–28°53′N, 76°50′–77°23′E) during May–June 2006. For the present investigation, ten sites in different undisturbed localities were randomly chosen for detailed observations. Phenoevents such as time of anthesis, anther dehiscence, flower longevity, period of flowering and fruiting were recorded. Anther dehiscence was determined by examining flowers (n = 30) under a stereomicroscope at different times, from the bud stage until anthesis between 0400 and 0800 h. Commencement of stigma receptivity and its duration were recorded through semi-vivo pollination studies[18]. Ovule production in a pistil was computed by scoring the cleared pistils (n = 30). Average pollen production in a flower (n = 30) was estimated using a haemocytometer[19]. Fertility of pollen grains was tested by scoring their stainability with 1% acetocarmine[18]. Pollen viability was assessed through fluorochromatic reaction test[20]. Pollen viability period was determined using pollen grains sampled every 60 min following anther dehiscence, till it declined to zero. The nature of reserve material in the pollen grains was identified using Sudan black for lipids and potassium iodide for starch.

As the flowers were visited only by snails and honey bees, detailed field observations were confined to these foragers. The standard entomological method was employed for collecting and preserving the honey bees[21]. To prevent the drying of snails during sampling, they were narcotized by asphyxiation, followed by washing thoroughly with distilled water to remove the mucous, passed

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through ascending ethanol series (20, 40, 60 and 70%) and finally stored in 70% ethanol[16] for identification. The samples were sent to the Zoological Survey of India, Kolkata for identification.

The role of floral visitors in pollination and their efficiency was ascertained on the bases of foraging behaviour, flower-handling time, pollen load and the number of pollen grains deposited on the stigma after their visit. For computing the stigmatic pollen load on the freshly opened flowers and after the visits of the foragers, flowers (n = 20, each site) were collected in dry screw-cap vials (2 ml), and their stigmas were mounted in a drop of auramine O′ and observed under an epifluorescence microscope (Nikon, AXII Optiphot). Foraging period and flower-handling time were recorded separately for each forager from all the study sites (a total of 90 h of observation). The average amount of pollen load on each floral forager (snails, n = 300; honey bees, n = 200) was counted by removing the pollen grains with a brush on separate clean microslides under the stereomicroscope (Nikon, SMZ 800), staining with auramine O′ and examining them under the epifluorescence microscope.

To ascertain whether or not the visit of snails and bees could lead to subsequent fruit- and seed-set, the flowers

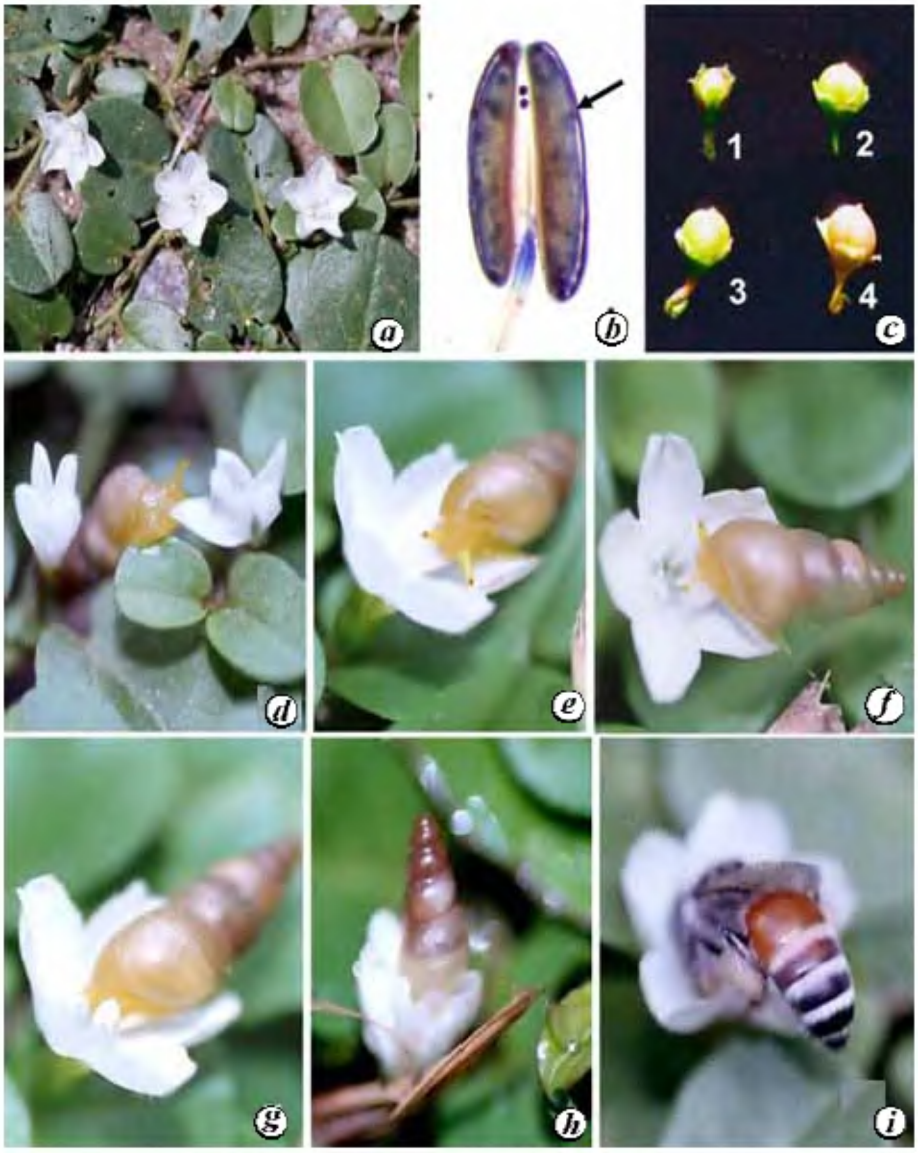

Figure 1. ***a***, Close-up of *Volvulopsis nummularium* plant showing prostrate habit with open flowers. ***b***, Whole mount of a stamen showing latrorse (arrow) longitudinal line of dehiscence of the anther. ***c***, Fruits with variable number of seeds (1–4). Fruit size is proportional to seed number. ***d–g***, Pollination mechanism in *V. nummularium*. ***d***, A snail approaches the flowers at anthesis. ***e***, It gradually crawls towards the anthers to forage. ***f***, The shell comes in contact with the dehisced anthers and pollen grains get adhered to the last whorl. ***g***, Pollen transfer occurs when the snail visits the next flower. ***h***, A snail entering a partially opened flower during a rainy day. Note vertical orientation of the shell. ***i***, A honey bee foraging the flower.

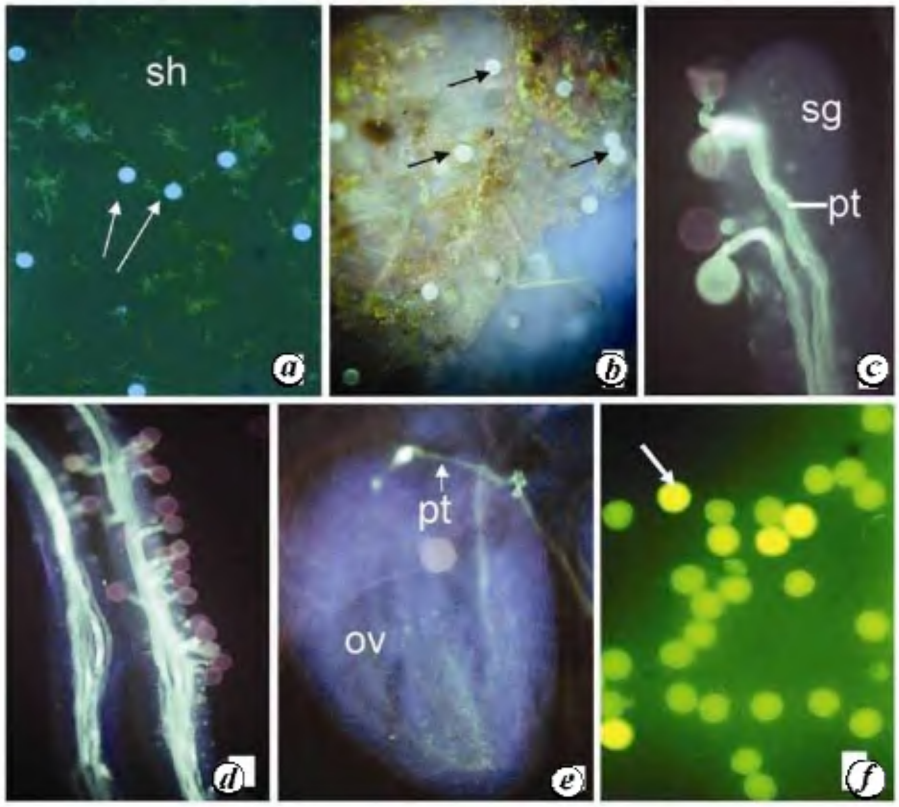

Figure 2. ***a–f***, Epifluorescence photomicrographs. ***a***, Auto-fluorescing pollen grains on the shell (sh) of a snail. ***b***, Freshly ingested pollen (arrows) in the gut of the snail. ***c***, ***d***, Pollen germination on the stigma (sg), and pollen tube (pt) growth after pollination by snail and honey bee respectively. ***e***, Entry of pollen tube (pt) into the ovule (ov) after hand-self pollination. ***f***, Pollen viability after 5 h; only the brightly fluorescing pollen grains (arrow) are viable.

were bagged after their first visit (n = ~500 each) and kept under observation for fruit-set. Interfloral movement of the foragers in a flowering patch was independently analysed for snails and bees on separate occasions (at five study sites) over a period of two months. Honey bee activity was traced by following the individual bee (n = 200) till it left a patch of plants, whereas the snails were marked with a dot of red on their shells for following their interfloral movement. The extent of phytophagy by snails was ascertained by recording the type of floral parts consumed, and also by dissecting the snails and examining the contents of their gut under the microscope.

Fruit- and seed-set through open pollination was computed by tagging the floral buds (n = 540) 12 h before anthesis. Any incidence of apomixis was ascertained by bagging (with transparent paper bags, 4 × 2 cm) the emasculated flowers (n = 220) 12 h before anther dehiscence. For assessing spontaneous autogamy, flowers were bagged without emasculation. Hand-self (forced autogamy) and cross-pollinations (xenogamy) were performed to ascertain the extent of self-incompatibility, if any, in the species. Self-compatibility index (SCI)[22] was computed based on these results. For all statistical purposes, SPSS12 was used. One-way ANOVA was employed for determining any significant difference in fruit- and seed-set between pollination treatments. The percentage values were arc-sine transformed before subjecting to ANOVA.

Flowering in *V. nummularium* occurred in a synchronous and seasonal manner at all the study sites. On bright and sunny days, flowers anthesized between 0700 and 0800 h, and remained open until noon. On rainy days, anthesis was delayed by ~60 min. and the flowers remained only partly opened (Figure 1 *h*). The corolla was slightly twisted in the bud and after complete opening, it assumed a sub-rotate shape (Figure 1 *a*, *e–g*). The corolla measured 6.66 ± 0.28 mm across in a fully opened flower. Flowers were odourless and lacked nectar.

During anthesis, five epipetalous stamens diverged from the throat of the corolla tube. The pistil is made up of a superior, unilocular ovary with four ovules borne on the basal placenta, and an inconspicuous style with a four-lobed stigma (6.2 ± 1.3 mm in length). Anther dehiscence occurs simultaneously with anthesis by a longitudinal line of dehiscence. The pollen grains were presented latrosely (Figure 1 *b*). On an average, each flower bore 968 ± 12 pollen grains and ~96.3% of them were fertile. The fresh pollen grains were primarily lipidic, sticky and exhibited 93% viability. Viability dropped to <3% within 5 h (Figure 2 *f*).

Table 1. Comparison of results of fruit- and seed-set following different modes of pollination

Pollination treatment	% Fruit-set (n)	F	Average number of seeds in a capsule (n)	F
Open-pollination	74.5 (540)	–	2.60 ± 0.04 (402)	–
Spontaneous autogamy	51.8* (158)	4.67	1.73 ± 0.11* (82)	2.03
Manual self-pollination (forced autogamy)	70.6* (551)	3.28	2.32 ± 0.04* (389)	1.98
Manual cross-pollination (xenogamy)	82.7* (503)	1.18	3.3 ± 0.06* (416)	0.06
Snail-pollination (malacophily)	74.4 (504)	n.s.	3.4 ± 0.06* (375)	1.26
Bee-pollination (melittophily)	89.4* (503)	0.88	3.6 ± 0.08* (450)	1.01

*Values significantly different at $P = 0.05$, when independently compared with open pollination using one-way ANOVA; $df = 9$; n.s, Difference with open-pollination not significant.

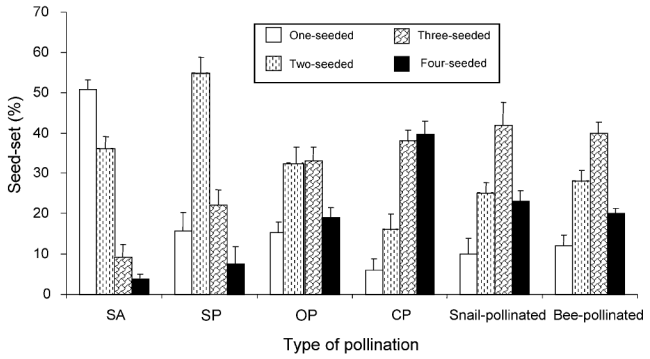

Figure 3. Effect of type of pollination on fruits bearing 1, 2, 3 or 4 seeds (percentage). (SP, Manual self-pollination; SA, Spontaneous autogamy; OP, Open-pollination; CP, Manual cross-pollination).

The stigma lobes were dry and non-papillate[23]. Stigma receptivity was attained before the opening of flowers at 0630 h and lasted till 1130 h. The pollen to ovule ratio was 241 : 1.

Flowers were visited by the terrestrial garden snail (*L. gracile*; Figure 1 *d–h*), and honey bees (*Apis cerana indica*; Figure 1 *i*). The population size of snails in the soil in which the plants were growing was approx. 30–50 per sq. m. Forging activity of both animals resulted in pollen transfer to the stigma, pollen germination and eventual fertilization and fruit-set (Figures 2 *c–e* and 3).

On sunny days foraging occurred in a successive manner; snails came first followed by honey bees. Snails foraged flowers between 0700 and 0900 h, and each snail spent 10 ± 3.3 min in a flower (n = 43). While consuming the pollen grains and anthers, the head, foot and broader portion of the shell (last whorl) of the snail came in contact with the dehisced anthers and stigma lobes, and effected pollen transfer (Figure 1 *e*, *f*). Foraging behaviour, gut analysis after fresh foraging of flowers (Figure 2 *b*) and faecal analysis showed that the snails primarily consumed the whole stamen or only the pollen grains. A snail carried approx. 180 ± 14.2 (n = 87) pollen grains on its shell (Figure 2 *a*). The average pollen count on the stigma of the snail-visited flowers (n = 30) was 95 ± 8.7. 75% (n = 504). Nearly 74% of snail-visited flowers developed into fruits (Table 1).

Honey bees visited the flowers between 0800 and 1100 h. On an average a honeybee spent only a brief period (4.2 ± 1.26 s) in a flower. Interestingly, the bees completely avoided flowers being foraged by snails or those that had been previously visited by the snails. However, the reverse was not true; snails readily foraged bee-visited flowers. Honey bees collected the pollen grains sternotribically on their thorax and hind legs in the form of pollen baskets. On an average each bee carried 2516.8 ± 47.64 pollen grains on its body parts. The stigmas of honey bee-visited flowers (n = 45) showed 123 ± 17 pollen grains and ~90% fruit-set occurred in the honey bee-visited flowers (n = 503 flowers; Table 1).

On rainy days, anthesis was delayed by 30 min and flower buds opened only partially. On such days, honey bee activity was totally absent. However, snails were active and forcibly entered the partly opened flowers (Figure 1 *h*) and foraged for a longer duration (18 ± 5.6 min, n = 28 flowers) than usual.

Flowers that were bagged after emasculation showed no fruit-set, thus ruling out pseudogamous form of apomixis. However, fruit-set resulted from other modes of controlled pollination (Table 1). The average number of pollen grains on the stigma of flowers that were bagged to assess spontaneous autogamy was as low as 11.2 ± 1.7 (n = 37) and spontaneous autogamy resulted in nearly 51% fruits (n = 158 flowers), with a seed-set of 1.73 ± 0.11 per capsule (Table 1). The percentage fruit-set through spontaneous autogamy was significantly lower than that resulting from other modes of pollination. Similarly, manual autogamy resulted in considerably lower seed-set in a

capsule than that resulting from open-pollination and xenogamy. The SCI value was 0.7.

The number of seeds ranged from one to four in each capsule (Figure 1 *c*). Based on the proportion of seeds in a fruit, the response among different pollination categories that yielded fruits was variable (Figure 3). The proportion of three- and four-seeded fruits was highest in manually cross-pollinated flowers (Figure 3). The difference in seed-set pattern between malacophily and melittophily was statistically insignificant.

We have clearly established the incidence of snail pollination in *V. nummularium* based on: (i) presence of a large number of snails in soil inhabited by the plants, (ii) foraging pattern of the snails, (iii) presence of pollen load on their body parts, (iv) occurrence of a larger number of pollen grains on the stigma of snail-visited flowers compared to natural autogamy, and (v) development of a high proportion of fruits and seeds in snail-visited flowers. These studies adequately fulfil the requirements of the postulates[24,25] formulated to establish whether or not a flower-visitor is a pollinator. The habit and habitat of the plant and the presentation of essential organs in the flowers conform to the floral traits suggested for malacophilous pollination syndrome[12,13,15]. Analysis of freshly digested floral parts in the gut of the snails and their faecal analyses clearly demonstrated their preference for pollen grains/anthers. Importantly, as the stigmatic lobes or other parts of the pistil are not consumed by snails, opportunity for pollination and fertilization is not diminished. Thus, snail-pollination is not destructive to the natural fecundity of *V. nummularium*.

Lipidic pollen was the sole floral reward for honey bees, whereas snails foraged pollen as well as anthers. Avoidance of snail-visited flowers by bees could be due to the lack of a landing platform or absence of floral reward. It is also likely that the slimy trail left by a snail on the flower could have dissuaded the bees.

Values of pollen : ovule ratio[26] and SCI[22] obtained through controlled pollinations, suggest that the mating system in the species is facultative autogamous. However, selfing is not sufficiently effective through the spontaneous mode. This is indicated by the poor pollen load on the stigmas of flowers not visited by any floral foragers and lower fruit and seed-set. These findings indicate that stigma lobes do not effectively come in contact with the latrorsely dehisced anthers. Pollination efficiency (stigmatic pollen load) is significantly increased with the participation of snails and honey bees. Although the latrorse pollen presentation may serve as an important contrivance to prevent autogamy in hermaphroditic and self-compatible plants, in those species in which the pollen grains and the stigma are presented simultaneously, flower-visitors may cause 'facilitated selfing' and outcrossing or geitonogamy in a single pollination act[23]. Such mixed deposition of pollen is likely to produce mixed progeny in the population. As the snails forage restrictively to patches below which they inhabit, their pollination activity may result largely in either selfed or geitonogamous progenies. However, xenogamy may also be brought about by snails when branches from the neighbouring plants overlap, bringing together flowers of different plants. Xenogamy is expected to be more prevalent in honey bee-pollinated flowers.

Pollination in the family Convolvulaceae is primarily by bees, although there are instances of pollination by moths, birds and bats[27]. The discovery of malacophily in *V. nummularium* is thus a novel addition to the pollination syndromes prevailing in the family. Pollination mechanism in *V. nummularium* represents an unusual guild that involves a polylectic interaction. Although snails are not the exclusive pollinators for ensuring fruit-set in the plants, they play a significant role in the pollination effort, especially on rainy days when the activity of bees is completely lacking. Adoption of snail as a pollinator, therefore, enables pollen transfer even on rainy days. We infer that these pollination strategies of natural autogamy to a limited extent followed by snail and/or bee pollination in *V. nummularium*, are of adaptive significance in achieving reproductive success without resorting to obligate selfing. This rare instance of malacophily points to the need to examine rainy-season flowering plants or those inhabiting water bodies more thoroughly, for a better understanding of the role of snails in pollination.

1. Richards, A. J., *Plant Breeding System*, George Allen and Unwin, UK, 1986.
2. Kearns, C. A., Inouye, D. W. and Waser, N. M., Endangered mutualism: The conservation of plant–pollinator interaction. *Annu. Rev. Ecol. Syst.*, 1998, **29**, 83–112.
3. Corlett, R. T., Flower visitors and pollination in the Oriental (Indo-Malayan) region. *Biol. Rev.*, 1998, **79**, 497–532.
4. Buchmann, S. L. and Nabhan, G. P., *The Forgotten Pollinators*, Island, Washington DC, 1996.
5. Kevan, P. G., Pollination biology and plant breeding systems. In *Pollen Biotechnology for Crop Production and Improvement* (eds Shivanna, K. R. and Sawhney, V. K.), Cambridge University Press, UK, 1997, pp. 59–84.
6. Roubik, D. W., *Pollination of Cultivated Plants in the Tropics*, Agricultural Service Bulletin 118, Food and Agriculture Organization, Rome, Italy, 1995.
7. Ackerman, J. D., Abiotic pollen and pollination: Ecological, functional and evolutionary perspective. *Plant Syst. Evol.*, 2000, **222**, 167–185.
8. Sussman, R. W. and Raven, R. H., Pollination of flowering plants by lemurs and marsupials: a surviving archaic coevolutionary system. *Science*, 1978, **200**, 731–736.
9. Flemming, T. H. and Sosa, V. J., Effects of nectarivorous and frugivorous mammals on reproductive success of plants. *J. Mamm.*, 1994, **75**, 845–851.
10. Janson, C. H., Terborgh, J. and Emmons, L. H., Non-flying mammals as pollinating agents in the Amazonian forest. *Biotropica*, 1981, **13**, 131–136.
11. Carthew, S. M. and Goldingay, R. L., Non-flying mammal pollinators. *TREE*, 1997, **12**, 104–108.
12. Pammel, L. H. and King, C. M., Honey plants of Iowa. *Iowa Geol. Surv. Bull.*, 1930, **7**, 892–894.
13. McGregor, S. E., Pollinating agents and their comparative value. In *Insect Pollination of Cultivated Crop Plants*, Agriculture Handbook, USDA, 1976, vol. 496, pp. 19–23.

14. Atwood Jr, J., How is *Paphiopedilum* pollinated? *Am. Orchid. Soc. Bull.*, 1982, **51**, 1057–1058.
15. Faegri, K. and van der Pijl, L., *The Principles of Pollination Ecology*, Pergamon Press, Oxford, 1963.
16. Mitra, S. C., Dey, A. and Ramakrishna, *Pictorial Handbook: Indian Land Snails*, Zoological Survey of India, Kolkata, 2005.
17. Babu, C. R., *Herbaceous Flora of Dehra Dun*, CSIR, New Delhi, 1977.
18. Shivanna, K. R. and Rangaswamy, N. S., *Pollen Biology: A Laboratory Manual*, Springer-Verlag, Berlin, 1992.
19. Kearns, C. A. and Inouye, D. W., *Techniques for Pollination Biologists*, University Press of Colorado, Colorado, 1993.
20. Heslop-Harrison, J. and Heslop-Harrison, Y., Evaluation of pollen viability by enzymatically-induced fluorescence; Intracellular hydrolysis of fluorescein diacetate. *Stain Technol.*, 1970, **45**, 115–120.
21. Steyskal, G. C., Murphy, W. L. and Hoover, E. M., *Insects and Mites: Techniques for Collection and Preservation*, USDA, Wrappers, USDA Misc. Publ., 1986.
22. Lloyd, D. G. and Schoen, D. J., Self and cross-fertilization in plants. I. Functional dimensions. *Int. J. Plant Sci.*, 1992, **153**, 358–369.
23. Heslop-Harrison, Y. and Shivanna, K. R., The receptive surface of the angiosperm stigma. *Ann. Bot.* 1977, **41**, 1233–1258.
24. Cox, P. A. and Knox, R. B., Pollination postulates and two-dimensional pollination in hydrophilous monocotyledons. *Ann. Mo. Bot. Gard.*, 1988, **75**, 811–818.
25. Dafni, A., *Pollination Ecology: A Practical Approach*, Oxford University Press, New York, 1992.
26. Cruden, R. W., Pollen–ovule ratios: A conservative indicator of breeding systems in flowering plants. *Evolution*, 1977, **31**, 32–46.
27. Austin, D. F., Dissolution of *Ipomoea* series Anisomerae (Convolvulaceae). *J. Torr. Bot. Soc.*, 1997, **124**, 140–159.

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Do bio-shields affect tsunami inundation?

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Conversion of coastal sand dunes to plantations has intensified dramatically after the tsunami of December 2004, driven largely by the belief that bio-shields mitigated tsunami inundation. This assumption was tested using field-based mapping and remote sensing. A regression between the Normalized Difference Vegetation Index and inundation distance was non-significant, questioning the premise for large-scale bio-shield plantations, mostly *Casuarina equisetifolia*, an exotic timber with unquantified ecological impacts. These plantations may obliterate the natural sand dune ecosystems along the Coromandel coast, which are an important natural defence and provide a range of ecological goods and services.

Keywords: Bio-shields, coastal sand dunes, remote sensing, tsunami.

VEGETATIVE shelter belts or bio-shields received a great degree of attention in India after the tsunami of 26 December 2004, where they were credited with mitigating tsunami inundation. Particular attention was given to mangroves[1] and more recently, *Casuarina*[2–6]. The total area proposed[7–9] to be covered by the Tamil Nadu Forest Department alone was 4000 ha of *Casuarina* and 1400 ha of mangroves during the period 2005–07. *Casuarina* was the preferred species due to its easy availability, low cost and high survival rate. Initial publications supported these plantations, with Dahdouh-Guebas *et al.*[10] and Kathiresan and Rajendran[11] suggesting that vegetative shelter belts, particularly mangroves were effective defences against the tsunami.

However, Kerr *et al.*[12] re-analysed their data and showed that vegetative area explained less than 1% of the variation in human mortality. Chatenoux and Peduzzi[13] showed that among geomorphic configurations, a long and shallow proximal slope caused greater wave run-up. This has been demonstrated by others as well[13–17]. Thus shallow coasts such as Nagapattinam are more vulnerable than deep shelves such as those around Puducherry. Among biological configurations measured by Chatenoux and Peduzzi[13], areas behind sea grass seemed less heavily affected by the tsunami. They also found that mangroves appeared to have no effect on inundation.

Much of the confusion about role of vegetation as tsunami defence lies in the relationship between bathymetry, nearshore elevation, distance from coast and presence of biological 'protection' such as mangroves[13]. Evidence from the Nicobar Islands[18] questions the premise that vegetation can absorb the enormous energy dissipated by a tsunami, albeit the fact that some obstacle would be better than none.

The inundation caused by tsunami run-up was measured using a baseline corresponding to a coastline digitized from high resolution QuickBird satellite image comprising red and blue bands at 2.44 m, hybridized with a panchromatic band at 0.6 m. Images of 31 December 2004 were downloaded from the Pacific Disaster Centre site (http://www.pdc.org). River mouths and backwaters were digitized such that the coastline looped into them to ensure that the analysis took into account inundation observed along backwaters.

Inundation points were identified with local residents and their coordinates recorded using a Garmin-76 GPS

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