Floral resources, pollinators and fruiting in a threatened tropical deciduous tree

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Abstract

Aims

Nothapodytes nimmoniana (Family Icacinaceae) is a deciduous tree species distributed in Asia facing severe population decline. Wood chips from the tree are a source of camptothecin, a globally sought-after alkaloid with cancer-treating properties, and are harvested unsustainably in natural forests. We studied the pollination ecology of the species and asked if there are constraints in pollination and fruiting success in its natural populations. We also discuss the potential effects of wood extraction on pollinators and reproductive success in the population.

Methods

The study was carried out during the flowering season in two populations with varying exploitation levels, both located in the Protected Area Network in the Western Ghats of Karnataka State. We assessed floral resource availability and measured pollinator diversity and activity in the canopy from the perspective of the biology of the species. We quantified pollinator abundance and percent fruit set as a function of population density.

Important Findings

Flowers belong to the fly pollination syndrome and are open to visits by generalists such as *Apis dorsata* and *Trigona iridipennis*. Fruiting success did not vary between exploited and unexploited sites, but there was a significant difference in pollinator assemblage. In a lean male flowering year, fruit set was low, suggesting pollen limitation in the population. No fruiting was recorded in the second year at the site where trees were felled soon after the flowering period. We argue that when male floral resources are altered in exploited populations, pollinators of generalist nature may show a shift in foraging pattern. Also, generalist plants may be as susceptible to pollination loss as are specialist plants. The need for outcrossing in the species would probably exacerbate this vulnerability.

Keywords: fruit set • generalist • over-harvest • pollen limitation • pollinator assemblage

INTRODUCTION

Studies on the nature of the interactions between plants and their pollinators are important to understand the structure and dynamics of tropical forest ecosystems, and have helped clarify issues of regeneration and conservation of tropical forest resources (Bawa and Hadley 1990). Pollination mechanisms and reproductive output of tropical forest trees remain largely unknown due to the complexity of plant–pollinator interactions and the practical difficulties of quantifying these interactions in forest canopies (Ghazoul and McLeish 2001). In the past two decades, much research has been carried out on the changing pollination dynamics of wild plant populations in the context of habitat change and fragmentation (Bond 1994; Ghazoul and McLeish 2001; Lennartsson 2002; Murren 2002; Pandit and Choudhury 2001; Somanathan and Borges 2000). And yet, little is known of the effect of a specific exploitation threat on the pollination ecology of tree species facing direct or indirect population alteration from over-harvesting of plant parts. We address this issue with regard to a species from the Western Ghats of India that has come under a recent and sudden threat of declining population due to commercial exploitation.

Nothapodytes nimmoniana Graham (Family Icacinaceae) is a tropical deciduous tree occupying evergreen and deciduous

forests. Its natural populations face indiscriminate harvest for trade of their wood chips, the richest known source of campto-thecin (CPT), an anti-cancer drug component (Govindachari and Viswanathan 1972; Suhas *et al.* 2007; Vasudeva *et al.* 2004), and the threat status is endangered/vulnerable (IUCN 2003). CPT is the third most important alkaloid sought after by pharmaceutical companies around the world (Hombe-gowda *et al.* 2002). Over 20% of the wild populations of *Notha-podytes* in India have declined in the last decade (Ravikumar and Ved 2000), and the method of harvest is unsustainable—lopping branches or often the main trunk (Vasudeva *et al.* 2004).

Nothapodytes nimmoniana is dioecous, but some individuals are polygamous, with male, female and bisexual flowers (Vasudeva *et al.* 2004). Apart from a report on sexuality (Hombegowda *et al.* 2002, Sharma *et al.* 2010), there is no in-formation on the reproductive ecology of the species. We ex-amine aspects of floral display and reward, and ask if insect visitation is proportional to floral attractivity between the sex types. We investigate the mode of pollination in the species and hypothesize that it is fly-pollinated given the foetid smell-ing flowers.

While the primary objective is to study the pollination biol-ogy of the species in its natural populations, we also consider the importance of pollination phenomena in limiting fruit set as a function of disturbance. We use two study sites—one with no history of wood chips extraction either in the Forest Depart-ment records or local non-timber forest produce harvest record (Setty *et al.* 2008) and the other, facing indiscriminate harvest.

Pollinator limitation (Kearns and Inouye 1997; Rathcke and Jules 1993), reduced population viability (Ghazoul 2005) and reduced outcrossing rates in low flowering density populations (Murawski *et al.* 1994) have been reported from fragmented populations across the tropics.

Floral resource depletion and increased isolation of individ-uals caused from exploitation of plant resources could also cause a decline in pollinator abundance by affecting the forag-ing and movement patterns (Ghazoul and Uma Shaanker 2004) and consequently reproductive success in the species (Cunningham 2000; Jennersten 1988; Kearns and Inouye 1997; Murren 2002; Saunders *et al.* 1991; Steffan-Dewenter and Tscharntke 1999). Our study sites provide an opportunity to investigate the impact of varying population densities on pollinator assemblage and reproductive success. We hypothe-size that there would be a decrease in pollinator activity and percent fruit set in the exploited population where floral re-sources are altered as a result of over-harvesting of plant parts.

MATERIALS AND METHODS

Study species

Nothapodytes nimmoniana, formerly *Mappia foetida,* is a small spreading sub-canopy tree distributed in the dry and moist de-ciduous and evergreen forests of the Western Ghats of India, and in the eastern states of Assam and West Bengal. Global distribution data record it from Sri Lanka, Myanmar, Thailand

and Taiwan. Trees occupy the sub-canopy stratum in the forest and grow up to 12–20 m tall. Flowering initiates in end May or early June soon after leaf bud initiation, lasting >6 weeks. Fruits mature in mid-July into red-purple single-seeded berries and are bird dispersed (MV Sharma, personal observation).

Study sites

Natural history and reproductive ecology studies were carried out in the undisturbed populations (Site UE or unexploited) of Biligiri Rangan (B.R.) Hills Wildlife Sanctuary and a population in Dandeli Wildlife Sanctuary (Site E or exploited) was used for comparing data on pollinator assemblage and fruit set. In 2005 and 2006, field experiments were set up in two populations in Site UE (Doddasampige N 11° 57′ 07′′, E 77° 09′ 63′′ and Mal-kibetta N 11° 57′ 22′′, E 77° 08′ 68′′, elevation: 1210 m) sep-arated from each other by a distance of ~4 km, and one population in Site E (N 15° 10′ 11′′, E 74° 28′ 91′′, elevation: 612 m). Data from the two populations at Site UE were pooled for the purpose of analysis. B.R. Hills Sanctuary, where Site UE is located, is 540 km^2 in area and has large stretches of undis-turbed forests. The population at Site E was located in a Pro-tected Area but was close to the highway and two human settlements.

A locally made bamboo ladder was used to access the trees, and once in the canopy, insect foraging observations were made at close range with a pair of Pentax 6X2.1 binoculars. Hand pollination experiments were also conducted in the can-opy during the peak flowering period—the second week from flowering initiation.

Population density and disturbance

We calculated density of adult trees at the two sites in the first year using the quadrat sampling method; the quadrat size was 10×10 m. In Year 2, when we encountered large-scale lop-ping of trees in one of the sites, we quantified the number of coppices or cut stems in the populations and used it as an index of disturbance/exploitation. These values were explanatory variables in the analyses that followed to compare pollinator diversity and fruit set in the two sites.

Floral morphology and display

To determine the time of anthesis, we tagged 10 ready-to-open buds on 2 trees to observe the following day. Ovary transverse sections ($n = 20$) were taken to determine ovule number. Inflo-rescence size was estimated from counting individual flowers and buds in a given inflorescence ($n = 25$ of three female, three male and three polygamous trees each). A two-sample *t*-test in R 2.7 (R version 2.7.1 (C), Vienna, Austria, Ihaka and Gentleman 1996) was employed to test the difference between the number of flowers in male and female inflorescences to be correlated to visitation frequency of pollinators to male and female flowers.

Floral reward

To determine the period of stigma receptivity (that coincides with the period until which effective pollination can be

achieved in a flower), we conducted hand pollinations on female and bisexual flowers at 6-h intervals starting with anthesis. The pistils were fixed 24 h after pollination in FAA (formaldehyde: glacial acetic acid: 70% ethanol, 5:5:90 v/v/v) for later observing pollen germination and pollen tube growth using aniline blue fluorescence (Shivanna and Rangaswamy 1992). Nectar measurements were made directly from open flowers on the branches using 1-µl microcapillaries (Microcaps, Drummonds, UK).

To estimate pollen production, a mature but undehisced anther (n = 20 each from three male and three polygamous trees) was placed in a drop of safranin or auromine O and teased with a needle to eject the pollen grains. After removing the debris, the number of pollen grains was counted under the compound microscope. Pollen viability was assessed on alternative days beginning from the day of anthesis using the fluorescine diacetate test (Heslop-Harrison and Heslop-Harrison 1970).

Floral visitors

To calculate frequency of floral visits by insects, observations were made in half-hour blocks from 0600 to 1800 h on eight trees of which three were male, two female and three polygamous. In each observation unit, four to six inflorescences were observed simultaneously. We pooled this into three time periods: morning (0600–1000 h), mid-day (1000–1400 h) and afternoon (1400–1800 h). Since the data comprised of count of insect visits, a generalized linear model with a zero-inflated quasi-poisson distribution of the error term was fitted in R 2.7 to identify time period of the day most preferred by pollinators and the most frequently visited inflorescence type, the hypothesis being that males attract more visitors. Insects seen foraging were collected using a sweep net and immobilized with ethyl acetate vapours. They were identified in the Entomology Laboratory at the Ashoka Trust for Research in Ecology and the Environment (ATREE, India) to the level of Family or Genus. To identify potential pollinators, insect bodies were scanned under the stereomicroscope for pollen load.

Using genuine counts of individuals (insect abundance), we calculated Inverse Simpson diversity indices (Vegan package in R 2.7) for insect morpho-species encountered. We then used a two-sample *t*-test to test the mean diversity indices in the two sites as a function of density and disturbance.

Yellow Sticky traps of 5 × 10 cm (Growing Success Ltd., Wiltshire, UK) were hung near flowering twigs from dusk to dawn to look for nocturnal insect visitors (Armstrong 1997; Sakai 2001). To check for the possibility of wind pollination, we hung vaseline-coated standard microscopic slides in the canopy of the tree for 24 h and scanned under the stereo microscope for the presence of pollen.

Reproductive success

Natural fruit set was calculated by counting the total number of flowers on 24 inflorescences on 4 female trees and 24 mixed inflorescences on 3 polygamous trees where we left them tagged until fruit set. To estimate percent fruit set, we monitored these tagged inflorescences and counted raw, immature fruits after 2–3 weeks. Hand pollination experiments were carried out on (bagged) female and (emasculated and bagged) bisexual flowers using pollen from male flowers of the same tree or a different tree. In polygamous trees, we bagged 30 mixed inflorescences with female buds to test for self-pollination. As flowers were too small to be marked or tagged individually, we covered the whole inflorescence with butter paper bags after snipping away younger buds.

All percent fruit set data were transformed using square root–arcsin transformation before analysis. A two-sample test in R 2.7 was employed to test the difference between fruit set in hand-pollinated and open-pollinated flowers. Reproductive success as a function of density and disturbance index in the two sites was tested, again with a two-sample *t*-test.

RESULTS

Population density and distribution

In 2005, the two populations displayed comparable densities—at B.R. Hills (Site UE), we recorded a mean density of 3.61 individuals ($\pm$1.08 standard error (SE)) per quadrat, and at Dandeli (Site E), the density was 2.69 ($\pm$0.97 SE) individuals per quadrat. In Year 2, after trees were found cut down at Site E, we recorded the number of coppices and it was a mean 1.45 coppices ($\pm$0.73 SE) per quadrat, with a 54% decline in the stand density. In site UE, there were no coppices or cut trees recorded, indicating zero extraction.

Floral morphology and display

Flowers of *N. nimmoniana* are creamish, bowl shaped and foetid smelling. Ovary is monocarpellary, with two ovules inside. All the three sex types—male, female and bisexual—have a disc-shaped nectary between the petals and the ovary. Flowers open during the day—ranging from 0600 to 1400 h. The small flowers are arranged in large terminal corymbose panicles of 20–400 flowers, intensifying advertisement.

The difference in the floral display size in male and female inflorescences was statistically significant (two-sample *t*-test, $t = -3.64$, degrees of freedom (df) = 33, $P < 0.001$); male inflorescences had a larger display (mean no. of flowers = 182.8 $\pm$ 51.3 SE, n = 20) than the females (mean no. of flowers = 68.9 $\pm$ 17.7 SE, n = 20). In polygamous trees, female and bisexual flowers were negligibly few in number and they made their appearance in select inflorescences towards the end of the flowering season.

Floral reward

A single male flower remained open for one day, while a female flower for 1–4 days depending on pollination success: if pollinated on the first or second day of opening, the flower begins to senesce and if pollen has not landed on the stigma, the flower remained open longer. Nectar secretion varied from

0.88 ± 0.02 µl (n = 8) at 0700 h, to 0.25 ± 0.06 µl (n = 6) at 1600 h. Male flowers also offer more reward than females in terms of pollen in addition to nectar.

Mean pollen production in male anthers was 1009.6 ± 61.91 (n = 15) and in bisexual anthers 448.4 ± 185.9 (n = 12); females had sterile anthers.

Pollen viability lasted for >10 days from the day of opening.

Floral visitors

There were nectar hunters and pollen foragers on the flowers. Seventeen species were encountered across the two sites, with flies being the most frequent visitors (Fig. 1a). We found two species of Calliphoridae, one species of Syrphidae, the short-tongued Halictid bee, the stingless bee *Trigona iridipennis*, *Apis dorsata*, *Apis florea*, Sepsid flies, Lycaenid butterflies and five species of ants. The Empididae, Scathophagidae, Mirid bug and Pompilid wasp appeared to be predators foraging on flower parts. Of these, only *T. iridipennis*, *A. dorsata* and two Calliphoridae members showed pollen load on their body (Fig. 1b) and were treated as the four possible pollinators.

Pollen grains on insects were confirmed to be of *N. nimmoniana* by comparing with pollen from squashed anthers under the microscope. Data on visitation were fitted to a generalized linear model with a quasi-poisson distribution of the error
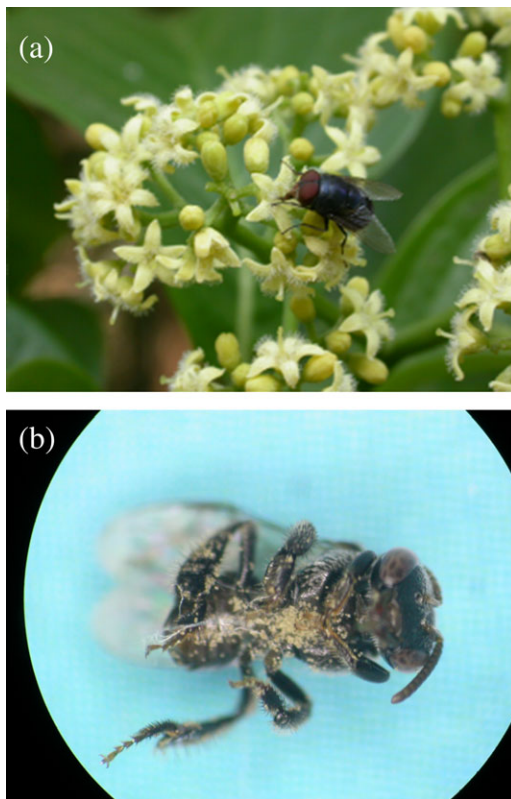
term and the simplified model revealed a highly significant influence of floral display (Z = 6.31, P < 0.001)—female inflorescences attracted significantly fewer number of pollinators compared to male and mixed inflorescences. Pollinators also showed a weakly significant preference for foraging during the morning (Z = 2.29, P = 0.023). Male flowers and morning hours showed a highly significant interactive effect (Z = –4.2, P < 0.001) (Table 1, Figs 2 and 3). Insect abundance and mean Inverse Simpson index were higher in Site E (two-sample t-test, t = –3.66, df = 48, P < 0.001) than in Site UE (Figs 4

Table 1: the minimal model derived from the generalized linear model fitted with a quasi-poisson distribution of the error term for the number of pollinator visits as a response to the variables inflorescence type and time of day

	Estimate	SE	Z value	$P(>|z|)$
Inflorescence female	0.69315	0.10977	6.314	<0.001***
Inflorescence male	0.26236	0.13616	1.927	0.0558
Inflorescence mixed	0.15415	0.11934	1.292	0.1984
Time evening	0.20972	0.12888	1.627	0.1057
Time morning	0.29725	0.12989	2.289	0.0234*
Inflorescence male: time evening	–0.30503	0.17201	–1.773	0.0781
Inflorescence mixed: time evening	–0.09724	0.14351	–0.678	0.4990
Inflorescence male: time morning	–0.76029	0.18092	–4.202	<0.001***
Inflorescence mixed: time morning	–0.22139	0.14619	–1.514	0.1320

Significant codes: 0'***' 0.001'**'0.01 '*'0.05 '.'0.1 ' '1 (dispersion parameter for quasi-poisson family taken to be 0.151932). Null deviance: 29.200 on 160 df; residual deviance: 24.729 on 152 df; Akaike Information Criterion: NA; number of Fisher scoring iterations: 4.
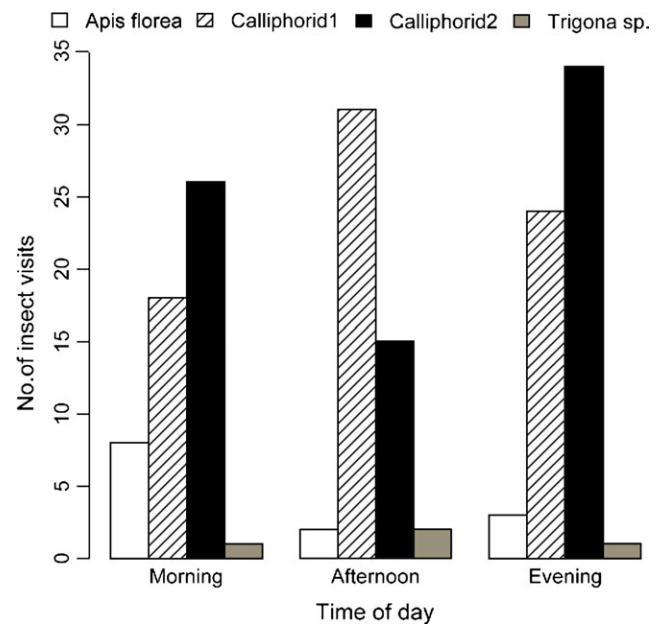

Figure 1: insects foraging on flowers of *Nothapodytes nimmoniana*: (**a**) Calliphorid fly, (**b**) Trigona bee under the stereomicroscope with pollen load on its ventral side.

Figure 2: insect foraging preference against time of day in *Nothapodytes nimmoniana* as recorded in B.R. Hills Wildlife Sanctuary (the unexploited site).

and 5). Four species encountered in the unexploited site were not encountered in the exploited site—*T. iridipennis*, Halictid bee, Syrphid fly and the Pompilid wasp, one of them a potential pollinator (*Trigona* sp.). No insects were captured on the sticky traps laid on tree branches from dusk to dawn, thus ruling out nocturnal pollinators. Twenty-two percent of the vaseline-coated slides hung in the canopy of polygamous trees showed pollen on them, suggesting some role of wind in pollination at least within such individuals.
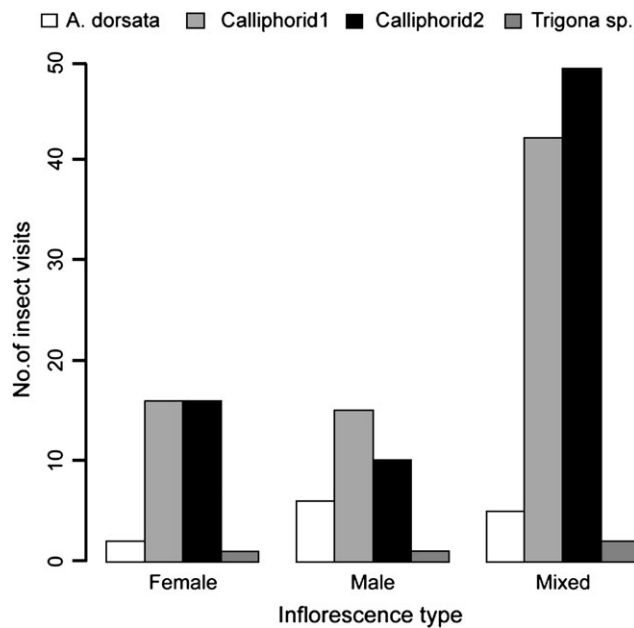

Figure 3: insect foraging preference against inflorescence type in *Nothapodytes nimmoniana* as recorded in B.R. Hills Wildlife Sanctuary (the unexploited site).
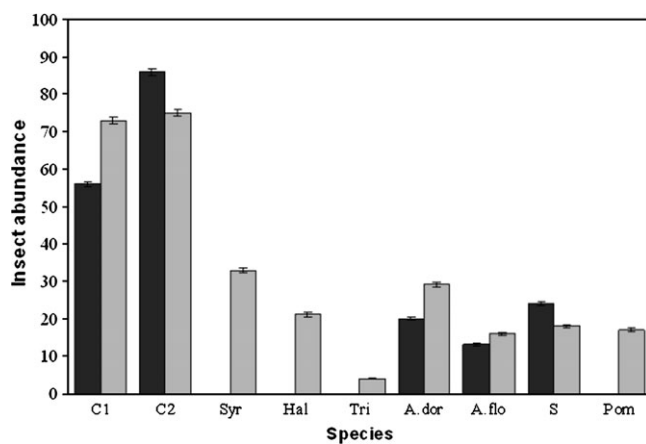
Reproductive success

There was considerable variation in the extent of fruit set between years in Site UE. In 2005, mean natural fruit set under open pollination in mixed inflorescences (on polygamous trees) was 40.94% and that in female inflorescences (on female trees) was 46.87%, with no significant difference (Student's *t*-test, $t = 1.35$, df = 46, $P = 0.18$). The mean fruit set in hand-pollinated female flowers in UE site was 49.16%, with no significant difference with that in open pollination (46.87%) (two-sample *t*-test, $t = 0.51$, df = 46, $P = 0.61$): a higher fruit set in hand-pollinated flowers would have indicated pollinator limitation. During the second year (2006), female inflorescences showed fruiting as low as 6.91% in comparison with 20.02% in mixed inflorescences with a significant difference in the means (Student's *t*-test, $t = -3.32$, df = 48, $P = 0.002$). In 2006, of the seven female trees marked, five did not have flowering male trees in the radius of ~50 m, causing a depletion in the male floral resource in the population. Eight of the 30 buds (26.67%) on polygamous trees netted to keep out visiting insects set fruit, indicating some natural self-pollination (geitonogamy).

In Site E, fruit set results in 2005 showed a weakly significant difference between hand-pollinated (46.4%) and open-pollinated (40.17%) flowers (Student's *t*-test; $t = 2.26$, df = 56, $P = 0.02$). The same year, comparing open fruit set in exploited and unexploited populations resulted in a non-significant difference (two-sample *t*-test; $t = -0.45$, df = 80, $P = 0.65$). During the second year, many of the trees we had marked were cut down soon after our flowering observations and thus no data on reproductive success for these trees were available. Several individuals were lopped back to the trunk leaving no branches to flower in the third year.
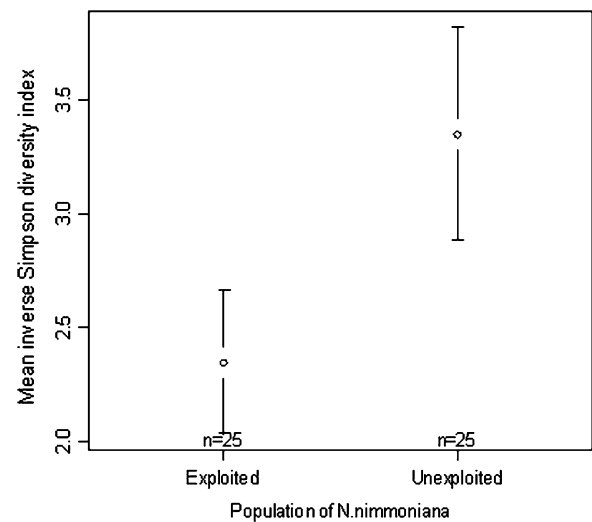

Figure 4: insect abundance in exploited (dark bars) and unexploited (light bars) populations of *Nothapodytes nimmoniana* in the Western Ghats, India. Insect families and species represented as C1 and C2: two Calliphorid species, Syr: Syrphid fly, Hal: Halictid bee, Tri: *Trigona iridipennis*, A.dor: *Apis dorsata*, A.flo: *Apis florea*, S: Sepsid fly and P: Pompilid wasp.

Figure 5: mean Inverse Simpson diversity indices of exploited and unexploited sites. The diversity index at Site E was significantly lower than Site UE (two-sample *t*-test, $t = -3.66$, df = 48, $P < 0.001$).

DISCUSSION

Natural history

Most of the findings of the study contribute to our understanding of the natural history and pollination ecology of a threatened species. The hypothesis that visitors may be more attracted to male inflorescences with higher floral productivity and floral reward was borne out, as is true for several tropical dioecious trees (Armstrong and Irvine 1989; Bawa 1980; Osunkoya 1999; Percy and Cronk 1997; Wilson 1979). Male inflorescences of *Nothapodytes* were larger than female inflorescences, offered more reward and were hence more attractive to foragers (Eckhart 1991; Grindeland *et al.* 2005; Huang 2006); this could be to assure pollen transfer (Bertin 1988; Harder and Barrett 1996; Hirabayashi *et al.* 2006; Ohashi and Yahara 1998). In female inflorescences, many flowers in close bunches open at one time, while in male inflorescences flowering is more spread out, presumably for higher and longer visual attractivity. Male *Nothapodytes* trees are a huge floral resource for insects and thus when a disappearance of male flowering branches/whole trees is encountered in the exploited study site, it points to a latent decline in pollinator activity.

Unspecialized visitors and wind are both characteristic of tropical dioecious trees (Charlesworth 1993). Flowers of *N. nimmoniana* conform to the non-specialized bees and fly pollination syndrome: small bowl/dish-shaped flowers, large inflorescence, dull colour and strong foetid odour (Baker and Hurd 1968; Faegri and van der Pijl 1979). Little research has been done to determine the role of flies as pollinators although there is literature that suggests flies as regular visitors or pollinators (Kearns and Inouye 1994; Moldenke and Lincoln 1979; Primack 1983). Flies appeared to be the most effective pollinators in our study. The species also seemed to attract typical generalists such as *A. dorsata*, halictid bee and *Trigona* sps.

The disturbance factor

Nothapodytes nimmoniana is reported to be facing severe decline in reproduction and regeneration in many populations across the country (Ravikumar and Ved 2000). The Dandeli population in our study presents a case of unsustainable harvest of wood chips by lopping tree branches from almost the base of their trunk, in effect not very different from timber extraction. During our second year of study, several trees in the population were lopped leaving no fruits behind and consequently no seeds on the forest floor to establish a new cohort.

There is only one population under the exploited category as against two unexploited populations in our study. We resolve this limitation in replication by taking into account the role played by provenance (geologically separated populations). Just as the two populations in Site UE fall under a single region of provenance, we do not expect that another population if sampled in Site E would show noticeable variation. In other words, we assume that a second or third population in Site E is 'within the provenance' since they share similar ecological

conditions (Kleinschmit *et al.* 2004). Although not all factors that contribute to variation within and among provenances are accounted for by geological and climatic parameters, in studies concerning pollen dispersal (Bergin *et al.* 2008) this assumption is justifiable as long as regular environmental conditions exist (Schoppa and Gregorius 2001).

We thus make valid comparisons between the samples from exploited and unexploited areas, suggesting that the differences that have emerged in pollinator assemblage may well represent patterns of exploited versus unexploited. Although it cannot be concluded that any difference is down to disturbance, we suggest that over-exploitation and alteration of the mating population may be part of the explanation of the difference observed.

Generalist systems in degraded populations

It has been raised that habitat conversion can reduce the abundance and diversity of insect pollinators (Rathcke and Jules 1993) and our results provide some evidence in this direction. Two generalist species Halictid bees and *T. iridipennis* were not encountered in the population with high density of coppices. We acknowledge that the diversity of floral visitors, besides being influenced by altered floral resources from disturbance, would be equally affected by factors such as proximity of a bee nesting site. And, although the lack of these insects in the exploited site does not seem to have a visible impact on fruit set, it might be a pointer to the depression in the pollinator community when there is a sharp floral resource decline, and in particular to the likely habitat loss of solitary and stingless bees in disturbed forest systems. Many floral generalists are in fact specialists for high density resources; low intensity flowering or spatial isolation of flowering individuals can make even the generalist insects susceptible to extinction (Pimm and Pimm 1982). In times of floral resource decline, generalist pollinators such as flies and bees might show a decreased foraging preference for the target species and switch to other flowering species in the forest (Murcia 1996; Somanathan and Borges 2000), leading to reduced visitation, less pollen reaching flowers, fewer fruits/seeds produced and in turn poor recruitment (Aizen and Feinsinger 1994; Harris and Johnson 2004; Jennersten 1988).

Ashworth *et al.* (2004) uses asymmetry in plant—pollinator systems (i.e. a specialist interacting with a generalist) in forest communities as a plausible explanation of why specialist and generalist plant species respond similarly to habitat fragmentation (Aizen *et al.* 2002) as against the expected pattern of specialized interactions being more prone to reproductive failure (Waser *et al.* 1996). Recent studies (Bascompte *et al.* 2003; Vazquez and Aizen 2004) have demonstrated that generalist plants are often pollinated not only by specialists but also by generalist pollinators, while specialist plants tend to be pollinated mostly by generalist animals. Thus, according to Ashworth *et al.* (2004), loss of many or all of their specialist pollinators places generalist plants in as susceptible a position as specialists. In the same vein, being a generalist does not make

N. nimmoniana less vulnerable to impacts of habitat disturbance, especially when the pollinator assemblage appears a mix of specialist and generalist and when little is known about the community-level plant–pollinator networks in forests of the region.

Fruiting success

The fruit set in experimentally pollinated flowers was not higher than open pollinated flowers, suggesting no pollinator limitation in the population. Comparison of percent fruit set between exploited and unexploited populations showed no significant difference; yet, we discuss here some notable aspects of fruiting dynamics in the two sites studied. When floral resources are scarce as in the lean male-flowering year, even the unexploited population with no extraction suffered a drastically low fruit set (6.91%). The situation would not be different in a population like Dandeli, where 54% of the trees were felled; there would be a gap between flowering individuals and flowering years, causing pollen limitation. In the same year, the polygamous individuals of site UE (those carrying flowers of male, female and bisexual flowers) showed a higher fruit set (20.02%) than female trees (6.91%), evidently because there was self-pollination in these individuals. In the entire population, only about 7% of the trees encountered were polygamous and the population is predominantly outcrossing (Sharma *et al.* 2010), making the species prone to the effect of lower flowering density and distribution (Bawa 1990). Comparing fruit set in the lean and good flowering seasons in Site UE gives an insight into the possible effect of spatial isolation of male individuals from cutting trees on the reproductive success in a dioecious species.

Populations in danger

There are at least three other populations of *Nothapodytes* in the deciduous forests of Dandeli Wildlife Sanctuary where exploitative harvest has been recorded (R. Vasudeva, personal communication). This pattern of harvest of tree trunks in vulnerable sites leaving large gaps in flowering between individuals and years is sufficient cause for conservation concern. *Nothapodytes* inhabits dry and moist deciduous forests of the Western Ghats—unique in vegetative characteristics and holding a greater diversity of birds and mammals than evergreen forests. These habitats are under an alarming rate of degradation, facing pressures from fire, grazing and large projects of mining and dams (Rawat *et al.* 2001).

Changes in floral resource intensity from exploitation of plant resources, the kind encountered in *N. nimmoniana*, could affect the mating structure of species and lead to a dip in seedling recruitment (Somanathan and Borges 2000). It may be argued that frequent selfing in *Nothapodytes* is advantageous in coping with pollinator decline, but that is no reason for complacency since our study demonstrates the vulnerability of these plant populations to anthropogenic pressure and the impact of disturbance on insect diversity. Further, different pollinator species may respond to land use changes such as lack

of habitat connectivity at different spatial scales (Steffan-Dewenter *et al.* 2001) and possibly varying time scales too.

CONCLUSIONS

In common with species with unspecialized flowers, *N. nimmoniana* flowers attract a generalist range of pollinating agents, although flowers display fly-pollination syndrome. Being largely a dioecious species, pollination success and seed set are dependent on the distribution of male trees in the neighbourhood of female species. When flowering male trees are lean in the neighbourhood of female trees, pollination becomes a major limitation. We found lower diversity and abundance of pollinators in the exploited site in comparison to the unexploited site, but this was little pressing evidence. Long-range studies may be needed to conclusively bring out the relationship between pollinators and habitat disturbance in a species with generalist pollination system such as *N. nimmoniana*.

Nothapodytes nimmoniana remained an obscure tree from the biodiversity-rich tropics until it became economically valuable to human use, endangering native populations from exploitative harvest of wood. A single-species approach can provide answers to intrinsic questions related to reproduction in a population and help predict plant species responses to disturbance (Ashworth *et al.* 2004). Such information, combined with studies on regeneration, is potentially valuable to recommend and develop strategies such as enrichment *in situ* or *ex situ* conservation (Shivanna *et al.* 2008). The case for conserving tropical plant and insect species needs to be re-evaluated by taking into account interactions in forest ecosystems along with the varying forces of anthropogenic threat.

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