Nucleated succession by an endemic palm *Phoenix pusilla* enhances diversity of woody species in the arid Coromandel Coast of India

Vijayalaxmi Kinhal1,2* and N. Parthasarathy1

1 Department of Ecology and Environmental Sciences, Pondicherry University, Puducherry 605014, India

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Abstract

**Background and aims**  
*Phoenix pusilla*, an endemic shrubby palm, was used as a model nurse plant in degraded tropical dry evergreen forest (TDEF) landscapes. This choice was informed by traditional ecological knowledge of the Irula tribe of south India. We tested whether the presence of *P. pusilla* in water-stressed arid regions improves conditions for other species to establish, resulting in nucleated succession. Success would point the way forward for establishing species-rich woodland in abandoned farm land on the south-eastern Coromandel Coast of India.

**Methodology**  
Spatial associations of woody species in the natural landscape were studied. Experimental tests of nurse plant potential examined the extent to which *P. pusilla* (i) promoted seed germination, (ii) seedling emergence and (iii) establishment of two TDEF species, and (iv) ameliorated soil and microclimatic conditions over 8 months.

**Principal results**  
*Phoenix pusilla* cooled the soil by up to 50% and decreased radiation by up to 9-fold, especially in summer. Soil organic matter and water-holding capacity increased, as did seedling number and seedling height of tested TDEF species. The presence of *P. pusilla* favoured a greater abundance (20%) of woody plants with a bias towards primary (11) rather than secondary (2) species, indicating species specificity of the effect.

**Conclusions**  
*Phoenix pusilla* ameliorated abiotic stresses present in open ground to create a patchy species-rich mosaic. This nucleated succession created using *P. pusilla* provided an important refuge for primary TDEF species. This effect can be expected to have impact at the landscape scale and may prove useful in managing landscapes and in biodiversity conservation. The conservation value of these patchy landscapes deserves to be more widely recognized as they persist in populated areas and thus merit protection. The value of traditional tribal knowledge in identifying a highly effective nurse species is highlighted by this study.

2 Present address: Institute of Bio-Architecture & Ecology, Udayan, Auroville Post 605101, Tamil Nadu, India

* Corresponding author’s e-mail address: vijayalaxmi.kinhal@gmail.com

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Introduction

Habitat modification by plants and its impact on other species

Positive interactions between plant species affected by inter-specific habitat modifiers can create new habitats by ameliorating stress (Jones et al., 1994, 1997; Bruno et al., 2003). By increasing spatial heterogeneity, positive interactions tend to increase diversity at the landscape or higher ecosystem levels (Jones et al., 1997). However, highly localized negative effects on diversity can also occur since negative and positive interactions between species can take place simultaneously. Overall, the net effect is positive under high environmental stress as the net effect of competition and facilitation usually shifts towards a positive effect on diversity when the severity of stress increases (Callaway and Walker, 1997; Michalet, 2006). When the stress and the benefits from positive interactions decrease, competition becomes more dominant; hence, facilitation and competition lie along a continuum of interactions (Bronstein, 1994; Stachowicz, 2001). As reviewed by Brooker et al. (2008), facilitation may depend on species identity, with the facilitated species commonly found at the extreme ends of their environmental tolerance, thus leading to range expansion. This pattern, in accordance with the stress gradient hypothesis (SGH) of Bertness and Callaway (1994), has been observed in plant interactions along aridity gradients (Aguiar and Sala, 1999; Gómez-Aparicio et al., 2004). Tielborger and Kadmon (2000) found that with increasing rainfall, the interactions changed from negative to neutral, and then to beneficial in desert herbs facilitated by shrubs. In contrast, the meta-analyses of Maestre et al. (2006) found no increase in either negative or positive interactions between plants under high abiotic stress in arid and semi-arid environments, although Lortie and Callaway (2006) disagreed with the findings due to limitations in the analytical approach, inappropriateness of some data sources and the selection criteria used for abiotic stress levels. Lortie and Callaway (2006) re-analysed the databases of Maestre et al. (2006) that led to conclusions in support of the SGH. Against this background, it is relevant to note that the strength of facilitation can increase both spatially and temporally during dry conditions (Gómez-Aparicio et al., 2004).

Nurse plants and stress amelioration

Most studies describing positive plant–plant interactions involve the use of nurse plants in conditions of high abiotic stress (Stachowicz, 2001). In degraded, arid environments, discontinuous plant cover can result, due to water limitation. The nurse plants change local biogeochernistry by creating spatial heterogeneity in a harsh landscape by affecting light penetration, hydrology, nutrient cycling and retention, erosion and sediment retention (Aguiar and Sala, 1999). Positive interactions on the microscale by nurse plants can create ‘islands of fertility’, facilitating patches of vegetation interspersed with bare ground by improving the availability of scarce resources such as mineral nutrients and moisture (Schlesinger and Plimanis, 1998; Aguia and Sala, 1999; Gillson, 2004). They also moderate extreme radiation levels and temperatures, thereby providing safer sites for germination, establishment and protection from herbivory (Vieira et al., 1994; Holl, 2002; Gómez-Aparicio et al., 2004). Once formed these islands influence spatial distribution of nutrients, which can affect other ecological processes as seen in the tree islands in the Everglades of Florida (Erin and Ross, 2010). A multiscale approach based on the hierarchical patch dynamics paradigm has shown that processes at lower level subsystems influence patterns of vegetation on a larger scale (Wu and Loucks, 1995). Fine-scale facilitation, combined with local scale factors of fire and herbivory, influenced patterning of vegetation at the landscape level in the African savannahs (Gillson, 2004). Thus, nurse plants can promote species that otherwise would not be recruited by helping to create refuges (Bertness and Yeh, 1994). In time, these refuges stabilize species richness and change species dominance, thus catalysing successional change (Badano et al., 2006).

Facilitation by nurse plants has been advocated in vegetation restoration projects, in highly disturbed environments (Brooker et al., 2008), and arid tropical and Mediterranean regions (Vieira et al., 1994; Gómez-Aparicio et al., 2004).

Nucleated succession

The fragmented tropical dry evergreen forest (TDEF) found along the eastern Coromandel Coast is one of the rarer forest types of India (Blanchflower, 2005). Forest species were reported to regenerate in clumps, in grazing lands near Puducherry (Kinhal and Parthasarathy, 2008a). Kellman (1980) hypothesized that nucleated succession was a possible mechanism of regeneration in such arid and degraded tropical land. Nucleated succession is a specific model of facilitated succession first proposed by Yarranton and Morrison (1974), and has been used to explain primary succession in sand dunes (Yarranton and Morrison, 1974; Franks, 2003) and secondary succession in pastures (Vieira et al., 1994) and salt marshes (Casal et al., 2001). Nucleation can occur due to species acting as perches for seed-dispersing birds or bats, or through facilitation by nurse plants, which...
involves amelioration of stress, augmentation of resources and protection from herbivory (Vieira et al., 1994; Suzán et al., 1996; Verdu and Garcia-Foyos, 1996; Bruno, 2000; Franks, 2003; Martinez, 2003). Studies from Amazonia and Costa Rica have shown that isolated shrubs and trees in abandoned tropical pastures have helped in regeneration of forest species outside forests through one or both means (Vieira et al., 1994; Hoil, 2002). However, identifying effective facilitator species is difficult (Jones et al., 1997). It is here that traditional ecological knowledge (TEK) can help. Since the 1980s, scientists have realized that local people’s ecological knowledge can be considerable and wide ranging (Berkes et al., 2000; Huntington, 2000), and this knowledge has been useful in projects aimed at maintaining species biodiversity, identifying rare species as well as recognizing and protecting key species (Gadgil et al., 1993; Berkes et al., 2000). However, TEK remains an under-used resource in science (Huntington, 2000), perhaps because it can sometimes be inaccurate and must be independently validated. In the present study, we sought guidance from the Irula, a hunter-gatherer tribe inhabiting the Coromandel Coast since pre-Dravidian times. Their knowledge of forest plants has been well documented and their herbal medicines are widely used (Madras Crocodile Bank, 2008; Methil, 2008).

**The present study**

*Phoenix pusilla* is an acaulescent (shrubby) palm, endemic to the Indian Coromandel Coast and locally abundant. It thrives in open sites, characterized by a vegetation mosaic, in clumps together with secondary vegetation mosaic, in clumps together with secondary shrubs and trees in abandoned tropical pastures. It is difficult (Jones, 2002). However, identifying effective facilitator species involves amelioration of stress, augmentation of resources and protection from herbivory (Vieira et al., 1994; Suzán et al., 1996; Verdu and Garcia-Foyos, 1996; Bruno, 2000; Franks, 2003; Martinez, 2003). Studies from Amazonia and Costa Rica have shown that isolated shrubs and trees in abandoned tropical pastures have helped in regeneration of forest species outside forests through one or both means (Vieira et al., 1994; Hoil, 2002). However, identifying effective facilitator species is difficult (Jones et al., 1997). It is here that traditional ecological knowledge (TEK) can help. Since the 1980s, scientists have realized that local people’s ecological knowledge can be considerable and wide ranging (Berkes et al., 2000; Huntington, 2000), and this knowledge has been useful in projects aimed at maintaining species biodiversity, identifying rare species as well as recognizing and protecting key species (Gadgil et al., 1993; Berkes et al., 2000). However, TEK remains an under-used resource in science (Huntington, 2000), perhaps because it can sometimes be inaccurate and must be independently validated. In the present study, we sought guidance from the Irula, a hunter-gatherer tribe inhabiting the Coromandel Coast since pre-Dravidian times. Their knowledge of forest plants has been well documented and their herbal medicines are widely used (Madras Crocodile Bank, 2008; Methil, 2008).

The main aim of the present study was to verify an Irula claim that *P. pusilla* can be an effective nurse plant for primary and secondary tree species in deforested and degraded TDEF areas. The TEK was collected in an informal semi-directive interview with 10 Irula women and men from three villages.

We also wished to identify the mechanism of any such facilitation by focusing on the following experimental objectives: (i) to identify whether *P. pusilla* is naturally associated with other woody species in regenerating areas of the Coromandel Coast; (ii) to quantify the extent to which *P. pusilla* changes the surrounding aerial and below-ground microclimate in comparison to open interspaces; and (iii) to establish whether *P. pusilla* can promote germination, seedling emergence and establishment of experimentally sown seeds of two primary forest tree species (*Walsura trifolia* and Diospyros ferrea).

**Materials and methods**

**Study area**

The vegetation of the Coromandel Coast is a TDEF (Type 7/C1) and a tropical dry evergreen scrub (Type 7/DS1) (Champion and Seth, 1968). It extends over a 500-km-long and 50-km-wide area from Ramanathapuram in the south to Vishakhapatnam in the north (Blanchflower, 2005). Physiognomically, it occurs as scrub-woodland or dense continuous thicket (Meher-Homji, 1973). However, rapid urbanization has resulted in only 4% of the original area remaining under forest cover (2002 data) and, of this, only 5% is pristine (Blanchflower, 2005).

**Climate**

The region has an average dry period of 6–8 months with a mean annual rainfall of $1033 \pm 69.79$ mm. Climate data for Puducherry from 1992 to 2002 reveal a mean annual temperature of $29.5 \pm 2.45^\circ C$ (Mani and Parthasarathy, 2006).

**Data collection**

**Spatial association** To study spatial association, two sites of privately owned semi-natural scrub, 1 km apart, were selected. The first is located within the Pondicherry University Campus (12°1.48′N, 79°50.95′E) and the second in the village of Pillaiachavady (12°1.95′N, 79°50.75′E). Each was formerly a cashew plantation and had been left without intercultivation for 20 years, allowing natural regeneration. At each site, a 1-ha plot was demarcated (50 m × 200 m) and 25 randomly placed subplots of $20 \text{ m} \times 5 \text{ m}$ ($100 \text{ m}^2$) were sampled. All individuals of woody species were recorded and placed into three height categories (<0.5, 0.5–1 and >1 m). To detect association within and between species, the nearest neighbour of each plant was recorded based on the ‘plant’s eye view’ method (Yarranton, 1966) as the plant with which it has physical above-ground contact or, in the absence of contact, on occurrence under the canopy shade. Plant identification and nomenclature followed Matthew (1991).

**Testing the efficacy of *P. pusilla*** The hypothesis that *P. pusilla* is an effective nurse plant was tested at the scrubs in Pondicherry University Campus and in Lakeside (11°57.70′N, 79°45.39′E), 12 km west of Puducherry (formerly Pondicherry). Although shrubby palms such as *P. pusilla* usually occur in clumps together with trees, it was possible to select nine palms at each site that were not associated with trees. For 8 consecutive months, including the stressfully hot
and dry period from May to June, soil temperatures at a depth of 20 mm and air temperatures at 1 m above ground level were measured every 4 weeks between 12:00 and 14:00 h with a Testo 920 remote probe thermometer (Testo, Gmbh & Co., Lenzkirch, Germany). In addition, light intensity was also measured during the same time interval, with a TES 1332 digital luxmeter (TES Electronic Corporation, Taiwan) every 2 weeks. Thirty-six soil cores (100 mm × 100 mm × 100 mm) were obtained once, for the analysis of water-holding capacity (WHC) and organic matter content (OMC). The WHC (%) was determined by oven drying a pre-weighed soil sample at 105 °C for 48 h after allowing for water absorption overnight. Organic matter (% dry wt) was estimated using a loss-on-ignition method, in which soil was burnt in a muffle furnace at 550 °C for 2 h (Dean, 1974). All measurements coincided with the locations of the seedling germination experiment, as described below, under each of the 18 selected palms and in nearby open areas at both test sites.

**Seedling germination, establishment and vigour** Seeds of the primary forest tree species *W. trifolia* and *D. ferrea* were obtained from the seed bank of Shakti, a unit of Auroville, Kottakuppam, Tamil Nadu, India. In mid-November 2007, 10 seeds of each species were sown 10–20 mm deep in the soil under each palm and ~2 m away on open ground. A total of 720 seeds were sown (20 seeds × 2 microsites × 9 palms × 2 sites), and the germination and seedling counts were made almost every 2 weeks. Two laboratory germination trials, using 10 seeds of each species, were also conducted to estimate the maximum germination potential. Seedling vigour was estimated at the end of the experiment by measuring seedling shoot height.

**Statistical analysis** Hill’s number (H₀) and Shannon’s index (H) were used to describe diversity and spatial association of woody species at each site. Species that were recorded most often as neighbours were considered as dominant associates/nurse plants. Chi-square tests were used to compare the counts of tree species associated with the dominant species and those found in open areas, with a significant difference leading to an inference of facilitation by dominant species. Where the trees species had less than 10 individuals, their numbers were pooled and classified as primary and secondary species for the chi-square test. Intra-specific association in *P. pusilla* was also determined by chi-square testing on numbers of individuals between clumps and open ground. Soil was analysed for difference in OMC and WHC by fitting a generalized linear mixed-effects model (GLMM), taking the experiment (‘under clump’ vs. ‘open ground’) as fixed factor, and the two sites and nine plants as random factors. Since light intensity and temperature readings have temporal pseudo-replication, GLMM were fitted, considering the months as continuous random factors, and site and nine plants as categorical random factors. The fixed factors in GLMM were ‘under clump’ vs. ‘open ground’ for light intensity analysis, whereas ‘under clump’ vs. ‘open ground’ and depth (soil) or height (air) were for temperature analysis. Germination results were tested by a generalized linear model (GLM) with quasi-Poisson errors, because the data showed over-dispersion. As no seedlings survived in the open at the University Campus site, seedling vigour was tested only for the Lakeside site by Student’s t-tests, using mean height of seedlings found under clumps vs. open microsites.

Data from the experiment were all analysed using the default mode of ‘R version 2.7.1’ statistical software (R core Development Team, http://www.r-project.org), after checking for normality and transforming when necessary.

**Results**

**Spatial association**

A total of 4101 individuals of 53 woody species were observed, composed of 15 shrubs, 15 lianas and 23 trees. The calculated diversity indices, H₀ and H, of all plants and according to arbitrary height classes are shown in Table 1, indicating only slight differences between the University Campus and Pillaichavady sites.

The species dominating inter-specific associations were the shrubs *P. pusilla* and *Dodonaea angustifolia*, followed by the trees *Azadirachta indica* and *Anacardium occidentale*, respectively (Table 2). The other species had negligible inter-specific association. Since *A. indica*...
is actually facilitated by *P. pusilla*, and *A. occidentale* (cashew) is a planted cash crop, only *P. pusilla* and *D. angustifolia* are considered as natural nurse plants. *Phoenix pusilla* exhibited the highest frequency of total association (21% of the total) as well as inter-specific association (14%). Results of the chi-square test (Table 3) indicate a significant positive facilitation of all primary forest species by *P. pusilla*, except *Chloroxylon swietenia*, which was more common in open ground. Although 10 of the 12 primary forest species associated with *P. pusilla* occurred only at very low numbers, chi-square test of their pooled individuals indicates a significant difference between ‘under clumps’ and ‘open ground’ sites. In contrast, the occurrence of secondary tree species was significantly higher in open ground, except *Acacia indica* and *Bridelia crenulata*, which are more associated with *P. pusilla* (Table 3). Chi-square tests also reveal that *P. pusilla* has a strong tendency to occur in aggregates (inter-specific association). Two primary species, which were found with *A. indica*, and *Tarenna asiatica* appear to be facilitated by *P. pusilla* indirectly (Table 3).

*Dodonaea angustifolia*, the second important associate species, has the tendency to facilitate five primary species (Table 3). Secondary tree species, such as *Acacia auriculiformis* and *A. holosericea*, were more common in open areas, whereas some species did not seem to exhibit any particular affinity with either of the dominant associates (cf. Table 3). All the liana species, except one, were associated with *P. pusilla* rather than *D. angustifolia*.

Initially, more plants of the smallest height category were found in open ground than with either dominant species. However, with growing height class, the beneficial effect of association becomes apparent. *Phoenix pusilla* can be considered as the more effective nurse plant species because of the large number of species and large number of individuals (Table 4) accumulating under it, and because these numbers increase with height class. This was not the case for *D. angustifolia*, although more individual plants grow in association with it than in the open.

### Amelioration of abiotic conditions

Soil WHC and OMC were significantly different under the clumps (WHC = 38.35%, OMC = 8.17% dry wt) than in open interspaces (30.91%, 6.89% dry wt) (see results of GLMM tests in Table 5). As expected, light intensity was markedly higher in the open areas (mean = 77 739.7 lux) than under clumps (mean = 9945.9 lux) (cf. Table 5, Fig. 1), but air temperature did not show any significant overall difference between University Campus (mean = 33.5 °C) and Lakeside (32.9 °C), and between clumps (31.7 °C) and open ground (31.2 °C) (Fig. 2). Indeed, no significant difference was detected.
### Table 3 Evaluating the efficiency of nurse plants. Results of chi-square tests on counts of associated species with *P. pusilla* and *D. angustifolia* under clumps and in open ground

| Association | Open area | *Phoenix pusilla* | \(\chi^2\) |
|-------------|-----------|-------------------|------------|
| **Primary forest species** | | | |
| *Atalantia monophylla*<sup>a</sup> | 0 | 1 | 3.156*** |
| *Canthium dicoccum*<sup>a</sup> | 0 | 2 | |
| *Cassia fistula*<sup>a</sup> | 4 | 1 | |
| *Cissus quadrangularis*<sup>a</sup> | 0 | 1 | |
| *Diospyros ferrea*<sup>a</sup> | 0 | 2 | |
| *Gymnema sylvestre*<sup>a</sup> | 0 | 3 | |
| *Ixora pavetta*<sup>a</sup> | 1 | 1 | |
| *Sapindus emarginatus*<sup>a</sup> | 0 | 1 | |
| *Strychnos minor*<sup>a</sup> | 0 | 1 | |
| *Wattakaka volubilis*<sup>a</sup> | 0 | 1 | |
| *Chloroxylon swietenia* | 45 | 23 | 7.78*** |
| *Tarenna asiatica* | 7 | 47 | 28.16**** |
| **Subtotal** | 57 | 84 | 4.79* |
| **Secondary species** | | | |
| *Acacia leucophloea*<sup>b</sup> | 0 | 1 | |
| *Breynia vitis-idaea*<sup>b</sup> | 0 | 4 | 3.2 NS |
| *Azadirachta indica* | 21 | 45 | 8.02*** |
| *Bridelia crenulata* | 0 | 18 | 16.05**** |
| *Acacia auriculiformis* | 80 | 31 | 22.52**** |
| *Acacia holosericea* | 223 | 44 | 121.35**** |
| *Phoenix pusilla* | 22 | 290 | 228.5**** |
| *Morinda pubescens* | 7 | 6 | 0.31 NS |
| **Subtotal** | 331 | 149 | 69.77**** |

#### Dodonaea angustifolia

| Association | Open area | *Dodonaea angustifolia* | \(\chi^2\) |
|-------------|-----------|-------------------------|------------|
| **Primary forest species** | | | |
| *Atalantia monophylla*<sup>a</sup> | 0 | 1 | |
| *Canthium dicoccum*<sup>a</sup> | 0 | 1 | |
| *Diospyros ferrea*<sup>a</sup> | 0 | 3 | |
| *Gymnema sylvestre*<sup>a</sup> | 0 | 2 | |
| *Tarenna asiatica* | 7 | 16 | 2.78 NS |
| *Chloroxylon swietenia* | 45 | 237 | 129.36**** |
| **Subtotal** | 52 | 267 | 140**** |
| **Secondary species** | | | |
| *Acacia auriculiformis* | 80 | 31 | 22.52**** |
| *Acacia holosericea* | 223 | 60 | 95.03**** |
| *Azadirachta indica* | 21 | 5 | 11.12*** |

Continued
between soil (mean = 31.4 °C) and air (35.0 °C) temperatures, but soil temperature tends to be much cooler under the clumps (29.8 °C) than in the open ground (40.3 °C) (cf. Table 5, Fig. 2).

**Seedling germination, establishment and vigour**

Field germination trials were consistent in their trends but less successful than the laboratory trials, where the germination of *D. ferrea* (10 %) was much lower than that of *W. trifolia* (55 %). In the field, only three *D. ferrea* emerged under the clumps at the campus site but did not survive the summer heat. Only seedlings of *W. trifolia* survived after 8 months. Survival rates were 25 % under canopy shade and 0.03 % in the open interspaces (Fig. 3). Therefore, results for the two species were combined. The GLM test (Table 5) showed that the emergence of seedlings was significantly less in the open ground (mean = 0.56) than under *P. pusilla* clumps (5.06). At the Lakeside site (Fig. 4), where some seedlings survived in the open, seedling height under *P. pusilla* (mean = 54.1 mm) was greater than in the open (26.5 mm).

**Discussion**

*Phoenix pusilla* forms intra-specific clumps in open areas, a phenomenon claimed by Kinhal and Parthasarathy (2008b) to be linked to the need for shade by young seedlings. These clumps of thorny, dome-shaped shrubby palms grow progressively larger and can reach 25 m in diameter, causing neighbouring clumps to coalesce. In natural conditions, this appears to promote succession through the role of *P. pusilla* as nurse plant (Aguiar and Sala, 1999). Similar nucleated succession of woody species has been reported for sand dunes (Yarranton and Morrison, 1974; Franks, 2003) and savannahs (Vieira et al., 1994). Results of our spatial analysis indicate that *P. pusilla* is the prominent habitat modifier at both study sites, facilitating more plant species directly and indirectly—including 11 primary forest species and 2 secondary species. In this respect, it is more effective than the other dominant associate, *D. angustifolia*, as a nurse species. Other studies have also recorded higher species diversity in areas with nurse plants (Mandujano et al., 2002;
Most secondary tree species, possibly due to shade intolerance, are more common in the open ground, whereas the primary species seem to have tolerance to shading and are thus facilitated by their association with *P. pusilla* (see also Suzán et al., 1996; Gómez et al., 2004). Thus, species specificity of interaction is based more on physiological and life-history traits of beneficiary species than on any specific effect of the nurse plant.

Both microclimatic and resource availability appear to be improved by *P. pusilla*. The soil became enriched with organic matter, a characteristic feature of nucleation and leading to better soil crumb structure (Schlesinger and Pilmanis, 1998; Aguiar and Sala, 1999; Casal et al., 2001; Gutierrez and Jones, 2006), although such a case was not observed elsewhere. For example, no improvement in OMC was found under nurse plants in subtropical Georgia and Florida, and in Mediterranean regions (Franks, 2003; Martínez, 2003; Gómez-Aparicio et al., 2008).

Soil temperatures were 1.35 times warmer in open interspaces than under *P. pusilla*. This observation is

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**Table 5** Amelioration of soil and microclimate under nurse plant. Results of GLMMs showing t-value and GLM with Poisson errors showing z-value

|                | Estimate | s.e.  | df   | t-value | P-value |
|----------------|----------|-------|------|---------|---------|
| **GLMMs**      |          |       |      |         |         |
| WHC            | Intercept| 38.349| 2.400| 17      | 15.973  | 0.0001  |
|                | Experiment (open) | −7.438| 2.803| 17      | −2.653  | 0.0167  |
| OMC            | Intercept| 8.174 | 0.733| 17      | 11.149  | 0.0001  |
|                | Experiment (open) | −1.189| 0.417| 17      | −2.848  | 0.0111  |
| Light intensity| Intercept| 39.349| 11.522| 412     | 3.415   | 0.0007  |
|                | Experiment (open) | 181.367| 6.493| 412     | 27.934  | 0.0001  |
| Temperature    | Intercept| 24.376| 0.791| 623     | 30.832  | 0.0001  |
|                | Experiment (open) | −0.467| 0.573| 623     | −0.813  | 0.416   |
|                | Depth    | −0.944| 0.573| 623     | −1.647  | 0.100   |
|                | Experiment: depth | 10.059| 0.441| 623     | 22.789  | 0.0001  |
| **GLM, with Poisson errors** |          |       |      |         |         |
| Seed germination| Intercept| 1.6205| 0.1048| 15.458  | 15.458  | 0.0001  |
|                | Experiment (open) | −2.2083| 0.3331| 15.458  | −6.628  | 0.0001  |

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**Fig. 1** Light intensity (lux) measurements under the *P. pusilla* clumps and in open interspaces at the University Campus (Uni) and Lakeside (Lake) scrubs.
consistent with those found in the tropical and Mediterranean regions (Martínez, 2003; Gómez-Aparicio et al., 2008), although there are exceptions (Gómez-Aparicio et al., 2005), with the size of nurse plants being one of the possible confounding factors (Kellman and Kading, 1992). However, the effect was large in our work and we thus conclude that \textit{P. pusilla}, as a nurse plant, has the ability to reduce the peak substrate temperatures, thus favouring the germination and growth of vulnerable seedlings (Holmgren, 1997) while slowing the drying of the soil (Shreve, 1931; Holmgren et al., 1997). Air temperature was not significantly affected in our work. While this accords with some work in the Mediterranean (Gómez-Aparicio et al., 2005), although not all (Gómez-Aparicio et al., 2008), cooler air temperatures that may have slowed evapotranspiration of young seedlings to their benefit have been reported (Franco and Nobel, 1989). The higher moisture content under nurse plants in the present study is similar to findings by Franks (2003) in the sub tropics, although some studies show no greater soil moisture under nurse plants in tropical and Mediterranean arid regions (Martínez, 2003; Gómez et al., 2008), while Kellman and Kading (1992) found that size and age of nurse plants effected the extent of any effect.

A year-round reduction in light intensity under \textit{P. pusilla} has been widely reported occurring under other nurse plants in the Mexican desert and coastal sand dunes (Valiente-Banuet et al., 1991; Martínez, 2003). Here, reduced radiation favoured germination (Valiente-Banuet et al., 1991), except for shade-intolerant species (Suzán et al., 1996), while slowing subsequent seedling growth (Franco and Nobel, 1989). However, some studies in temperate regions show no reduction in radiation by nurse plants (Gómez et al., 2005), although others have shown a size-dependent reduction (Kellman and Kading, 1992). The interaction of less radiation and better soil organic matter is reflected in the superior germination of \textit{W. trifolia} and \textit{D. ferrea} when under \textit{P. pusilla}. Higher survival of seedlings due to facilitation by other nurse plant species (Bruno, 2000; Gómez-Aparicio et al., 2005), including late successional grasses under \textit{Chamaecrista chamaecristoides} (Martínez, 2003), has been reported.

Seedlings of \textit{W. trifolia} survived under \textit{P. pusilla} and were almost twice the height of those in open areas.
interspaces (Fig. 4). A similar trend has been observed in cacti under nurse plant canopies (Mandujano et al., 2002). Stronger shoot elongation under shade may be the outcome of several effects including the red/far red balance (Pierik et al., 2004) and photoinhibition of photosynthesis (Gómez-Aparicio et al., 2006). Similarly, Casal et al. (2001) found that grasses germinating in open ground died without achieving reproduction, although the grasses under nurse plants survived to produce seeds. The efficacy of D. angustifolia as a nurse plant now needs to be substantiated further by experiments clarifying the mechanisms. Such work could usefully distinguish between impacts on the aerial or soil environments and less direct effects.

The spatial aggregation of other forest species with P. pusilla could be explained as a facilitative response to stress or, alternately, a nucleation process due to P. pusilla acting as perches for seed-dispersing birds or bats (Vieira et al., 1994; Verdu and Garcia-Fayos, 1996; Aguiar and Sala, 1999; Holl, 2002), trapping wind-blown seeds, enhancing suitability for growth by soil agglomeration (Bruno, 2000; Franks, 2003) or providing protection from herbivory for young seedlings (Gómez-Aparicio et al., 2008).

A total of 112 woody species, composed of 77 tree species (Mani and Parthasarathy, 2006) and 35 liana species (Reddy and Parthasarathy, 2006), have been recorded in the fragmented TDEF on the Coromandel Coast. However, the number of woody species in any given fragment ranges only from 6 to 36 (Parthasarathy et al., 2008). Since P. pusilla is associated with 11 primary forest species of the TDEF, its effect on the landscape may add significantly to species diversity and contribute to returning it to a level more typical of non-degraded fragmented TDEF. This role of P. pusilla as a nurse plant that initiates nucleation can be accepted, validating the Irula tribe’s understanding of the concept of a nurse plant and of ecological processes (Gadgil et al., 1993; Berkes et al., 2000). Although often dismissed merely as scrubland, areas occupied by P. pusilla need to be valued as possible refugia for a variety of threatened shade-tolerant forest species (Parthasarathy et al., 2008).

Conclusions and forward look

Phoenix pusilla, an endemic thorny acaulescent palm, was identified as a possible nurse plant with the help of traditional knowledge from the Irula tribe. It was found to be directly and indirectly associated with 11 primary forest and two secondary forest species, potentially increasing their distribution on a landscape scale. The amelioration of radiation, thermal and water stresses by P. pusilla changes the abiotic conditions of its habitat to one more favourable for the establishment of other woody species, through the process of nucleated succession. Existing patches of nucleated succession thus need protection to conserve primary forest species populations regenerated outside of the surviving forest fragments. To catalyse restoration, selection of future sites for restoration or conservation on the Coromandel Coast could usefully focus on P. pusilla-dominated landscapes. However, P. pusilla has other uses: fruits are edible, leaves are used for basket and mats, and roots are a fuel in lime making (Gamble and Fischer, 1915–1935; Basu and Chakravarty, 1994). Despite its obvious utility, P. pusilla is often considered a weed and cleared away. This practice needs to stop. Phoenix pusilla also deserves to be conserved in its own right, as it is endemic to the Coromandel Coast and found only over a few hundred square kilometres, overlapping the distribution of TDEF. When considering facilitation for conservation purposes, however, Garcia and Obese (2003) noted the importance of determining the consistency of facilitative effects by a nurse plant, such as P. pusilla, at a larger spatial scale in view of the implications of expanding the distribution and persistence of the few associated species over a wider range of the forest.

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Contributions by the authors

All the authors contributed to a similar extent overall.

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Conflict of interest statement

None declared.

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