



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

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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

biogeochemistry 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 Pilmanis, 1998; Aguiar 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-Fayos, 1996; Bruno, 2000; Franks, 2003; Martínez, 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; Holl, 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 keystone 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 and primary forest species interspersed in a matrix of herbaceous cover or bare soil (Kinhla and Parthasarathy, 2008a,b). 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 ± 69.79 mm. Climate data for Puducherry from 1992 to 2002 reveal a mean annual temperature of 29.5 ± 2.45 °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°1.487'N, 79°50.950'E) and the second in the village of Pillaichavady (12°1.953'N, 79°50.751'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 m × 5 m (100 m²) 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°57.700'N, 79°45.396'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 (H_0) 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, H_0 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*

Table 1 Hill's number (H_0) and Shannon's index of species diversity (H') at two study sites

Height category	Pillaichavady village		University Campus	
	H_0	H'	H_0	H'
0–0.5 m	24	0.972	29	0.911
0.5–1.0 m	22	1	32	1.042
>1 m	31	1.057	37	1.06
Total	38	1.075	40	1.043

Table 2 Identifying the inter-specific associates. Ten plants with the highest number of associations were considered as dominant species, and the proportion that was intra-specific and inter-specific was checked to find inter-specific facilitators

Dominant species	Association			
	Total numbers (%)	Intra-specific numbers	Inter-specific numbers (%)	% Total
No association	640 (16)	0	640 (100)	16
<i>Phoenix pusilla</i>	858 (21)	290	568 (66)	14
<i>Dodonaea angustifolia</i>	389 (13)	77	312 (86)	7.6
<i>Azadirachta indica</i>	270 (7)	3	267 (99)	7
<i>Anacardium occidentale</i>	259 (6)	15	244 (94)	6
<i>Tarenna asiatica</i>	97 (2)	5	92 (95)	2
<i>Acacia holosericea</i>	288 (7)	212	76 (26)	2
<i>Jasminum angustifolium</i>	101 (2)	28	73 (72)	2
<i>Chloroxylon swietenia</i>	355 (9)	299	56 (16)	1
<i>Acacia auriculiformis</i>	249 (6)	212	37 (15)	1
<i>Lantana camara</i>	58 (1)	25	33 (57)	1
Miscellaneous associations	377 (9)	0	377 (100)	9
Total density	4101	1166	2935	72

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 *A. 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 (intra-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	<i>Phoenix pusilla</i>	χ^2	
			Species	Subgroup
Primary forest species				
<i>Atalantia monophylla</i> ^a	0	1		
<i>Canthium dicoccum</i> ^a	0	2		
<i>Cassia fistula</i> ^a	4	1		
<i>Cissus quadrangularis</i> ^a	0	1		
<i>Diospyros ferrea</i> ^a	0	2		
<i>Gymnema sylvestri</i> ^a	0	3		
<i>Ixora pavetta</i> ^a	1	1		
<i>Sapindus emarginatus</i> ^a	0	1		
<i>Strychnos minor</i> ^a	0	1		
<i>Wattakaka volubilis</i> ^a	0	1		^a 31.56***
<i>Chloroxylon swietenia</i>	45	23	7.78***	
<i>Tarenna asiatica</i>	7	47	28.16****	
Subtotal	57	84		4.79*
Secondary species				
<i>Acacia leucophloea</i> ^b	0	1		
<i>Breynia vitis-idaea</i> ^b	0	4		^b 3.2 ^{NS}
<i>Azadirachta indica</i>	21	45	8.02***	
<i>Bridelia crenulata</i>	0	18	16.05****	
<i>Acacia auriculiformis</i>	80	31	22.52****	
<i>Acacia holosericea</i>	223	44	121.35****	
<i>Phoenix pusilla</i>	22	290	228.5****	
<i>Morinda pubescens</i>	7	6	0.31 ^{NS}	
Subtotal	331	149		69.77****
<i>Dodonaea angustifolia</i>				
Primary forest species				
<i>Atalantia monophylla</i> ^a	0	1		
<i>Canthium dicoccum</i> ^a	0	1		
<i>Diospyros ferrea</i> ^a	0	3		
<i>Gymnema sylvestri</i> ^a	0	2		^a 9.14***
<i>Tarenna asiatica</i>	7	16	2.78 ^{NS}	
<i>Chloroxylon swietenia</i>	45	237	129.36****	
Subtotal	52	267		140****
Secondary species				
<i>Acacia auriculiformis</i>	80	31	22.52****	
<i>Acacia holosericea</i>	223	60	95.03****	
<i>Azadirachta indica</i>	21	5	11.12***	

Continued

Table 3 Continued

Association	Open area	<i>Dodonaea angustifolia</i>	χ^2	
			Species	Subgroup
<i>Breynia vitis-idaea</i>	0	1	0.5 ^{NS}	
<i>Morinda pubescens</i>	7	11	0.5 ^{NS}	
Subtotal	331	108		112.26****
Subtotal	331	149		69.77****

Species pooled together for analysis due to low numbers are indicated by the letters a and b. NS, values not significant.

*Significant at $P < 0.05$.

***Significant at $P < 0.005$.

****Significant at $P < 0.001$.

Table 4 Species richness Hill's number (H_0) and density (Den) in three size classes, and chi-square test of all woody species facilitated by the nurse plants *P. pusilla* and *D. angustifolia* compared with open spaces. Plant height category: Ht-1, 0–0.5 m; Ht-2, 0.5–1.0 m; Ht-3, >1 m

	Ht-1		Ht-2		Ht-3		Total woody species			
	H_0	Den	H_0	Den	H_0	Den	H_0	Den	H_0 (χ^2)	Den (χ^2)
<i>Phoenix pusilla</i>	17	218	25	186	36	448	42	857	4.38*	31.17****
<i>Dodonaea angustifolia</i>	17	365	16	95	17	87	25	549	0.08 ^{NS}	6.81*
Open spaces	20	489	13	77	13	73	24	640		

NS, values not significant.

*Significant at $P < 0.05$.

****Significant at $P < 0.001$.

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

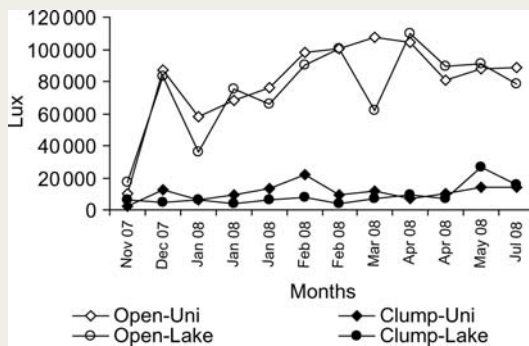
Field germination trials were consistent in their trends but less successful than the laboratory trials, where the germination of *D. ferrea* (10%) was much lower than that of *W. trifolia* (55%). In the field, only three *D. ferrea* emerged under the clumps at the campus site but did not survive the 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 (Aguar 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;

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
				z-value	
GLM, with Poisson errors					
Seed germination					
Intercept	1.6205	0.1048		15.458	0.0001
Experiment (open)	-2.2083	0.3331		-6.628	0.0001


Fig. 1 Light intensity (lux) measurements under the *P. pusilla* clumps and in open interspaces at the University Campus (Uni) and Lakeside (Lake) scrubs.

Franks, 2003; Martínez *et al.*, 2003), although in some cases there were variations in benefits depending on the size and age of nurse plants (Kellman and Kading, 1992; Suzán *et al.*, 1996).

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

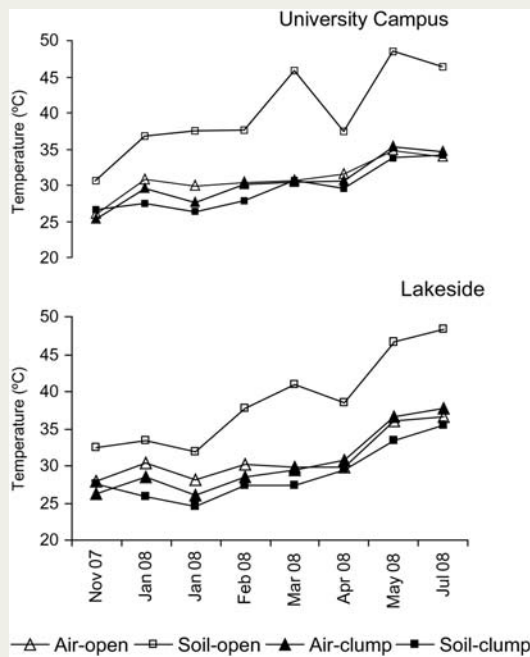


Fig. 2 Temperature variations in the experiment under the *P. pusilla* clumps and in open interspaces at the University Campus and Lakeside sites.

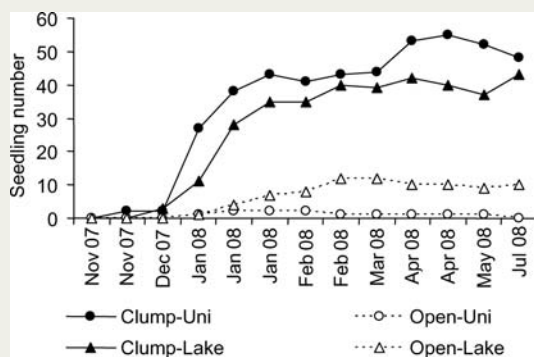


Fig. 3 Survival of *W. trifolia* and *D. ferrea* seedlings over 8 months in the University Campus site (Uni) and the Lakeside site (Lake) under *P. pusilla* and in open areas.

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 *P. pusilla*, as a nurse plant, has the ability to reduce the peak substrate temperatures, thus

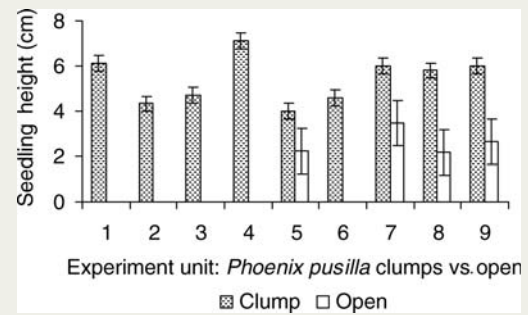


Fig. 4 Average height of *W. trifolia* seedlings under *Phoenix pusilla* clumps and in the open at the Lakeside site. Bars are standard errors.

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 subtropics, 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 *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 *W. trifolia* and *D. ferrea* when under *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 *Chamaecrista chamaecristoide* (Martínez, 2003), has been reported.

Seedlings of *W. trifolia* survived under *P. pusilla* and were almost twice the height of those in open

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.

References

- Aguiar MR, Sala OE. 1999. Patch structure, dynamics and implications for the functioning of arid ecosystems. *Trends in Ecology and Evolution* 14: 273–277.
- Badano EI, Jones CG, Cavieres LA, Wright JP. 2006. Assessing impacts of ecosystem engineers on community organization:

- a general approach illustrated by effects of a high-Andean cushion plant. *Oikos* **115**: 369–385.
- Basu SK, Chakravarty RK. 1994.** *A manual of cultivated palms in India*. Calcutta: Botanical Survey of India.
- Berkes F, Colding J, Folke C. 2000.** Rediscovery of traditional ecological knowledge as adaptive management. *Ecological Applications* **10**: 1251–1262.
- Bertness MD, Callaway RM. 1994.** Positive interactions in communities. *Trends in Ecology and Evolution* **9**: 191–193.
- Bertness MD, Yeh SM. 1994.** Cooperative and competitive interactions in the recruitment of marsh elders. *Ecology* **75**: 2416–2429.
- Blanchflower P. 2005.** Restoration of the tropical dry evergreen forest of peninsular India. *Biodiversity* **6**: 17–24.
- Bronstein JL. 1994.** Our current understanding of mutualism. *The Quarterly Review of Biology* **69**: 31–51.
- Brooker RW, Maestre FT, Callaway RM, Lortie CL, Cavieres LA, Kunstler G, Liancourt P, Tielbörger K, Travis JMJ, Anthelme F, Armas C, Coll L, Corcket E, Delzon S, Forey E, Kikvidze Z, Olofsson J, Pugnaire F, Quiroz CL, Saccone P, Schifffers K, Seifan M, Touzard B, Michalet R. 2008.** Facilitation in plant communities: the past, the present, and the future. *Journal of Ecology* **96**: 18–34.
- Bruno JF. 2000.** Facilitation of cobble beach plant communities through habitat modification by *Spartina alterniflora*. *Ecology* **81**: 1179–1192.
- Bruno JF, Stachowicz JJ, Bertness MD. 2003.** Inclusion of facilitation into ecological theory. *Trends in Ecology and Evolution* **18**: 119–125.
- Callaway RM, Walker LR. 1997.** Competition and facilitation: a synthetic approach to interactions in plant communities. *Ecology* **78**: 1958–1965.
- Casal RAE, Castillo JM, Luque CJ, Figueroa ME. 2001.** Nucleation and facilitation in salt pans in Mediterranean salt marshes. *Journal of Vegetation Science* **126**: 761–770.
- Champion HG, Seth SK. 1968.** *A revised survey of the forest types of India*. New Delhi: Government of India Press.
- Choler P, Michalet R, Callaway RM. 2001.** Facilitation and competition on gradients in alpine plant communities. *Ecology* **82**: 3295–3308.
- Dean WEJ. 1974.** Determination of carbonate and organic matter in calcareous sediments and sedimentary rocks by loss on ignition: comparison with other methods. *Journal of Sedimentary Petrology* **44**: 242–248.
- Erin JH, Ross M. 2010.** Across-scale patterning of plant-soil-water interactions surrounding tree islands in southern Everglades landscapes. *Landscape Ecology* **25**: 463–476.
- Franco AC, Nobel PS. 1989.** Effect of nurse plants on the microhabitat and growth of cacti. *Journal of Ecology* **77**: 870–886.
- Franks SJ. 2003.** Facilitation in multiple life-history stages: evidence for nucleated succession in coastal dunes. *Plant Ecology* **168**: 1–11.
- Gadgil M, Berkes F, Folke C. 1993.** Indigenous knowledge for biodiversity conservation. *Ambio* **22**: 151–156.
- Gamble JS, Fischer CEC. 1915–1935.** *Flora of the Presidency of Madras*. Vols 1–3. London: Adlard and Son.
- Garcia D, Obeso JR. 2003.** Facilitation by herbivore-mediated nurse plants in a threatened tree, *Taxus baccata*: local effects and landscape level consistency. *Ecography* **26**: 739–750.
- Gillson L. 2004.** Evidence of hierarchical patch dynamics in an East African Savanna. *Landscape Ecology* **19**: 883–894.
- Gómez-Aparicio L, Zamora R, Gómez JM, Hódar JA, Castro J, Baraza E. 2004.** Applying plant facilitation to forest restoration in Mediterranean ecosystems: a meta-analysis of the use of shrubs as nurse plants. *Ecological Applications* **14**: 1128–1138.
- Gómez-Aparicio L, Gómez JM, Zamora R. 2005.** Microhabitats shift rank in suitability for seedling establishment depending on habitat type and climate. *Journal of Ecology* **93**: 1194–1202.
- Gómez-Aparicio L, Valladares F, Zamora R. 2006.** Differential light responses of Mediterranean tree saplings: linking ecophysiology with regeneration niche in four co-occurring species. *Tree Physiology* **26**: 947–958.
- Gómez-Aparicio L, Zamora R, Castro J, Hódar JA. 2008.** Facilitation of tree saplings by nurse plants: microhabitat amelioration or protection against herbivores? *Journal of Vegetation Science* **19**: 161–172.
- Gutierrez JL, Jones CG. 2006.** Physical ecosystem engineers as agents of biogeochemical heterogeneity. *BioScience* **56**: 227–236.
- Holl KD. 2002.** Effect of shrubs on tree seedling establishment in an abandoned tropical pasture. *Journal of Ecology* **90**: 179–187.
- Holmgren M, Scheffer M, Huston MA. 1997.** The interplay of facilitation and competition in plant communities. *Ecology* **78**: 1966–1975.
- Huntington HP. 2000.** Using traditional ecological knowledge in science: methods and applications. *Ecological Applications* **10**: 1270–1274.
- Jones CG, Lawton JH, Shackak M. 1994.** Organisms as ecosystem engineers. *Oikos* **69**: 373–386.
- Jones CG, Lawton JH, Shackak M. 1997.** Positive and negative effects of organisms as physical ecosystem engineers. *Ecology* **78**: 1946–1957.
- Kellman M. 1980.** Geographical patterning in tropical weed communities and early secondary succession. *Biotropica* **12**: 34–39.
- Kellman M, Kading M. 1992.** Facilitation of tree seedling establishment in a sand dune succession. *Journal of Vegetation Science* **3**: 679–688.
- Kinhal V, Parthasarathy N. 2008a.** Secondary succession and resource use in tropical fallows: a case study from the Coromandel Coast of south India. *Land Degradation and Development* **19**: 649–662.
- Kinhal V, Parthasarathy N. 2008b.** Ecology of a dioecious palm *Phoenix pusilla* (Arecaceae), endemic to Coromandel Coast of India. *Indian Journal of Science and Technology* **1**: 1–7. <http://www.indjst.org>.
- Lortie CL, Callaway RM. 2006.** Re-analysis of meta-analysis: support for the stress-gradient hypothesis. *Journal of Ecology* **94**: 7–16.
- Madras Crocodile Bank. 2008.** <http://www.madrascrocodilebank.org> (September 2008).
- Maestre FT, Valladares F, Reynolds JF. 2006.** The stress-gradient hypothesis does not fit all relationships between plant-plant interactions and abiotic stress: further insights from arid environments. *Journal of Ecology* **94**: 17–22.
- Mandujano MC, Flores-Martínez A, Golubov J, Ezcurra E. 2002.** Spatial distribution of three globose cacti in relation to different nurse-plant canopies and bare areas. *The Southwestern Naturalist* **47**: 162–168.
- Mani S, Parthasarathy N. 2006.** Tree diversity and stand structure in inland and coastal tropical dry evergreen forests of peninsular India. *Current Science* **90**: 1238–1246.

- Martínez ML. 2003.** Facilitation of seedling establishment by an endemic shrub in tropical coastal sand dunes. *Plant Ecology* **168**: 333–345.
- Matthew KM. 1991.** *An excursion flora of central Tamil Nadu, India*. New Delhi: Oxford and IBH.
- Meher-Homji VM. 1973.** A phytosociological study of the *Albizia amara* Boiv. community of India. *Phytocoenologia* **1**: 114–129.
- Methil R. 2008.** Antidote to poverty: snake hunters learn to reconcile livelihood with respect for nature. Offtrack: India Today. <http://www.india-today.com/itoday/20000918/offtrack.shtml>. (September 2008).
- Michalet R. 2006.** Is facilitation in arid environments the result of direct or complex interactions? *New Phytologist* **169**: 3–6.
- Parthasarathy N, Selwyn MA, Udayakumar M. 2008.** Tropical dry evergreen forests of peninsular India: ecology and conservation significance. *Tropical Conservation Science* **1**: 89–110.
- Pierik R, Cuppens MLC, Voesenek LACJ, Visser EJW. 2004.** Interactions between ethylene and gibberellins in phytochrome-mediated shade avoidance responses in tobacco. *Plant Physiology* **136**: 2928–2936.
- Reddy MS, Parthasarathy N. 2006.** Liana diversity and distribution on host plants in four tropical dry evergreen forests of peninsular India. *Tropical Ecology* **47**: 103–116.
- Schlesinger WH, Pilmanis AM. 1998.** Plant–soil interactions in deserts. *Biogeochemistry* **42**: 169–187.
- Shreve R. 1931.** Physical conditions in sun and shade. *Ecology* **12**: 96–104.
- Stachowicz JJ. 2001.** Mutualism, facilitation, and the structure of ecological communities. *BioScience* **51**: 235–246.
- Suzán H, Nabhan GP, Patten DT. 1996.** The importance of *Olneya tesota* as a nurse plant in the Sonoran desert. *Journal of Vegetation Science* **7**: 635–644.
- Tielborger K, Kadmon R. 2000.** Temporal environmental variation tips the balance between facilitation and interference in desert plants. *Ecology* **81**: 1544–1553.
- Valiente-Banuet A, Bolongaro-Crevenna A, Briones O, Ezcurra E, Rosas M, Nunez H, Barnard G, Vazquez E. 1991.** Spatial relationships between cacti and nurse shrubs in a semi-arid environment in central Mexico. *Journal of Vegetation Science* **2**: 15–20.
- Verdu M, Garcia-Fayos P. 1996.** Nucleation processes in a Mediterranean bird-dispersed plant. *Functional Ecology* **10**: 275–280.
- Vieira ICG, Uhl C, Nepstad D. 1994.** The role of the shrub *Cordia multispicata* Cham. as a ‘succession facilitator’ in an abandoned pasture, Paragominas, Amazonia. *Vegetatio* **115**: 91–99.
- Wu J, Loucks OL. 1995.** From balance of nature to hierarchical patch dynamics: a paradigm shift in ecology. *The Quarterly Review of Biology* **70**: 439–466.
- Yarranton GA. 1966.** A plotless method of sampling vegetation. *Journal of Ecology* **54**: 2229–2237.
- Yarranton GA, Morrison RG. 1974.** Spatial dynamics of a primary succession: nucleation. *Journal of Ecology* **62**: 417–428.