SHORT COMMUNICATION

The understorey palm *Licuala* (Arecaceae) suppresses tree regeneration in a lowland forest in Asia

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The establishment and growth of a young tree requires a microsite that falls within a range of specific environmental conditions. Microsites will to some degree be modified by such neighbouring plants as are already established, a circumstance that will in turn lead to either a positive or negative spatial association among the individuals. Such patterns of spatial interactions are amenable to statistical inference. Positive associations may result when one species ameliorates overall hostile conditions, such as the shade and moisture provided the seedlings of long-leaf pine by the canopy of the saw palmetto (Allen 1956). Indeed, positive associations appear widespread in arid and cold habitats (reviewed in Tirado & Pugnaire 2003). However, on the forest floor of the humid tropics, negative associations are presumably more likely (Montgomery 2004). Harms *et al.* (2004) recently found a correlation between high density of small palms and a low density of tree saplings across four Neotropical sites, while Wang & Augspurger (2004) demonstrated that dwarf palms and cyclanths reduce seedling recruitment on the forest floor in Costa Rica.

We investigated the spatial co-occurrence of understorey palms in the genus *Licuala* (Arecaceae) with the saplings of trees recruited into a permanent plot of lowland tropical forest in Malaysia. *Licuala* is a genus of 110 species of long-lived, short-stemmed or caespitose palms indigenous to South-East Asia and the Western Pacific where they create a characteristic appearance within forest understorey (Saw 1994). They bear fan-shaped leaves with blades 1–2 m across and typically incised in wedge-shaped portions. The petioles range up to 3 m long

creating a dome-like canopy of foliage. Individual leaves can twist to optimize the intercept of light (Takenaka *et al.* 2001) and thereby augment the shade within the already shaded forest interior.

Between 1986 and 1989, all trees greater than 1 cm dbh were mapped, measured and identified in a 50-ha permanent research plot in lowland forest in Peninsular Malaysia (Kochummen *et al.* 1990, Manokaran & LaFrankie 1990, Manokaran *et al.* 1990). Trees that grew into the 1 cm dbh class after 1985 were enumerated in 1990, 1995 and 2000 and were labelled as recruits. They numbered 54365 and represented 739 species.

Between 1990 and 1993, over 17,226 palms representing three species of the genus *Licuala* were likewise mapped, identified and the leaves counted and measured (Saw 1994). Individuals of *Licuala* with mean petiole length over 2 m – i.e. large plants – numbered 8884 in the plot and included the two species *Licuala ferruginea* Becc. and *Licuala longipes* Griff. ex Mart.

Tabulations were made with SAS version 8.1. Point patterns were analysed using Ripley's K function (Dale 1999, Haase 1995, Plotkin *et al.* 2002, Ripley 1976) calculated with SPPA v 2.0 (Spatial Point Pattern Analysis. Version 2.0). The weighting approach, used to correct for edge effects (Getis & Franklin 1987 modified by Haase 1995) yields unbiased results for distances up to half of the shortest side of the plot. The null hypothesis of no spatial interaction was tested by randomly assigning locations to recruits while holding position of *Licuala* stationary. The distance *t* was evaluated from zero to 20 m at 1-m increments with 1000 randomizations providing a 99% confidence interval.

The two species of *Licuala* were spatially segregated according to topography (presumably in response to soil
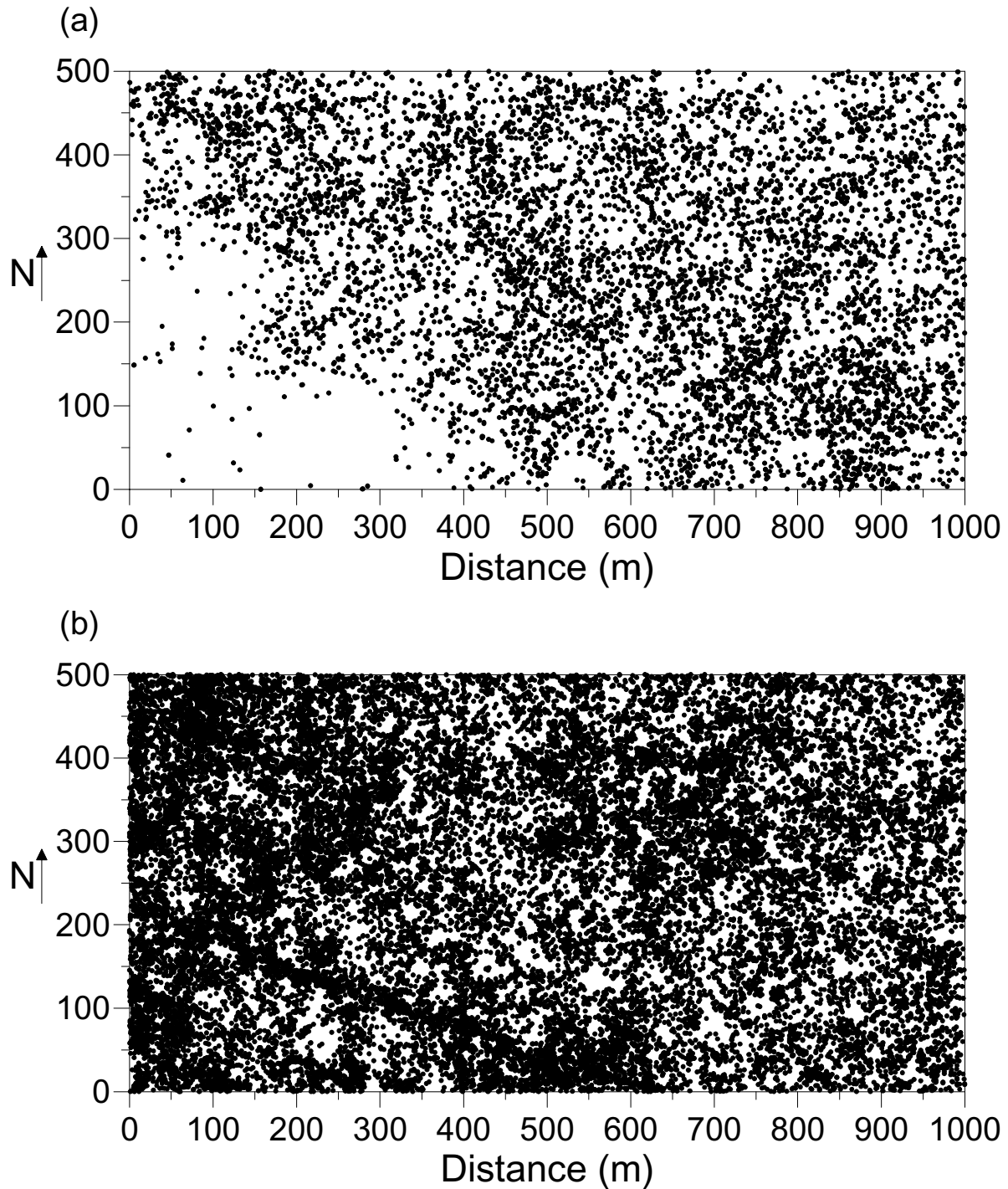
(a)

(b)

Figure 1. Location of 8884 *Licuala ferruginea* and *L. longipes* with mean petiole length ≥2 m in a 50-ha permanent plot in Pasoh Forest Malaysia (a); location of 54 365 tree saplings ≥1 cm dbh in that same plot (b).

moisture) and possibly with respect to soils (Saw 1994), while the combined species map showed low density in the south-west corner of the plot (Figure 1a) possibly due to the sandy well-drained soils that predominate there. Tree recruits were generally more abundant in the western half of the plot where the canopy was more broken (Figure 1a).

The correlation between number of recruits and number of large palms was negative but with great scatter ($r^2 = 0.132$) at the 1-ha scale (Figure 2). Those hectares that had very high numbers of recruits varied widely in the number of *Licuala* whereas hectares with fewer than 800 recruits all had more than 100 individuals of *Licuala*.
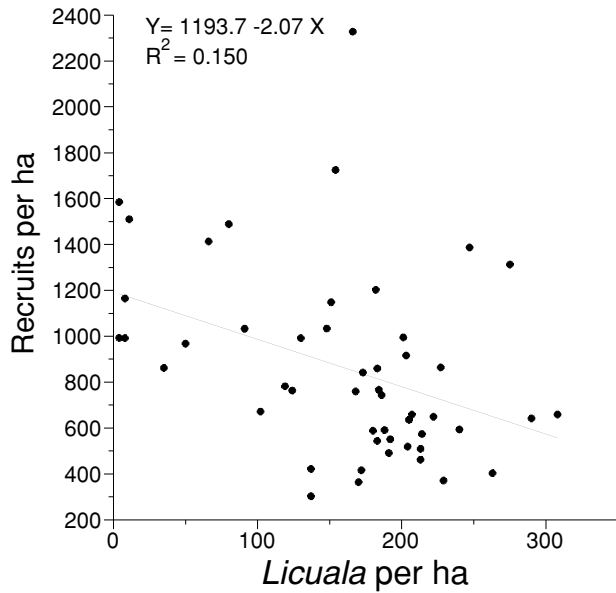
Figure 2. The number of trees newly recruited to the 1 cm dbh class between 1985–2000 fifty 1-ha squares vs. the number of individuals of *Licuala* (mean petiole length ≥ 2 m) in each ha.
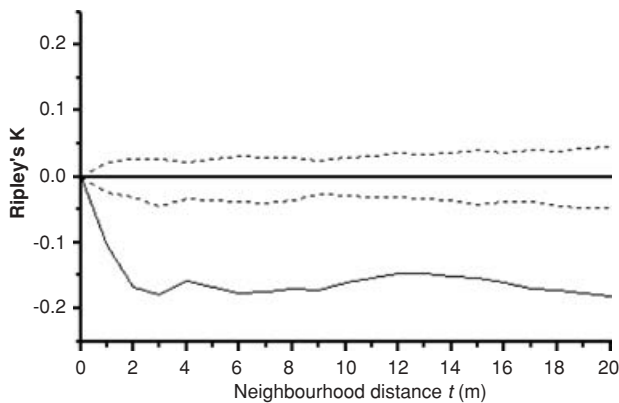

Figure 3. Second-order spatial analysis of the distribution pattern of *Licuala* spp. and tree recruits 1990–2000. The plot of the derived statistic of Ripley's K function vs, t shows negative association from neighbourhood distance t of 0–3 m and no increase thereafter. Dotted lines give 99% confidence intervals for complete spatial randomness from 1000 randomizations.

Using the central 9-ha square where both *Licuala* and recruits were abundant, we found a sharp and highly significant negative association from 0–2 m and a lesser reduction from 2–3 m (Figure 3). Beyond a distance of 3 m, no further influence of *Licuala* was seen.

The consequent pattern of the negative association is seen in the relative abundance of saplings within 3 m of *Licuala*. Within the 9-ha square, we found that locations within 3 m of a large *Licuala* represented 40.9% of the total area, but included only 10.2% of the recruits (2×2 table, df = 1, $\chi^2 > 4000$, P < 0.0001). We compared the species composition of the two classes, i.e. recruits within

3 m of a *Licuala* and recruits beyond 3 m and found no significant difference in either diversity (Fisher's alpha) or identity of the ten most abundant species. Neither were there significant differences in growth or mortality.

Shading is the most naturally suspected mechanism of suppressing sapling regeneration. Farris-Lopez *et al.* (2004) found that light availability beneath a midstorey palm was 27% lower than readings beyond the canopy, and that seedling numbers beneath the canopy were reduced 33% from background numbers. However, they also found that leaf litter was five times thicker below the canopy. Palms may also serve to make the local sites drier, or remove nutrients, although trenching experiments on seedlings near palms and cyclanths were not significant (Denslow *et al.* 1991).

The results provide a Palaeotropical complement to the recent evidence that the abundant understorey palms of the Neotropics can obstruct regeneration of trees (Farris-Lopez *et al.* 2004, Harms *et al.* 2004, Wang & Augspurger 2004), while they add to the list of factors known to create microsite heterogeneity on the forest floor. These factors now include: tree fall gaps and associated light (Dalling & Hubbell 2002, Dalling *et al.* 1998, Davies *et al.* 1998, Montgomery 2004, Turner 2001); leaf litter (Benítez-Malvido & Kossmann-Ferraz 1999) and larger debris from storms (Walker *et al.* 2003); the micro-biota that putatively direct strong local density dependence (Wills & Condit 1999); and larger biota that change the local composition of understorey treelets (Ickes *et al.* 2001, 2003; Levey & Byrne 1993).

While the results here confirm for the Paleotropics that understorey palms can suppress tree saplings immediately beneath their canopy, it does not necessarily follow that the removal of palms will boost regeneration. Only experimental trials can ascertain the balance between increased space and light provided by removal of palms against the desiccation that might be expected to follow, as well as unanticipated ecological consequences.

LITERATURE CITED

ALLEN, R. M. 1956. Relation of saw-palmetto to longleaf pine reproduction on a dry site. *Ecology* 37:195–196.

BENÍTEZ-MALVIDO, J. & KOSSMANN-FERRAZ, I. D. 1999. Litter cover variability affects seedling performance and herbivory. *Biotropica* 31:598–606.

DALE, M. R. T. 1999. *Spatial pattern analysis in plant ecology*. Cambridge University Press, Cambridge. 326 pp.

DALLING, J. W. & HUBBELL, S. P. 2002. Seed size, growth rate and gap microsite conditions as determinants of recruitment success for pioneer species. *Journal of Ecology* 90:557–568.

DALLING, J. W., HUBBELL, S. P. & SILVERA, K. 1998. Seed dispersal, seedling establishment and gap partitioning among tropical pioneer trees. *Journal of Ecology* 86:674–689.

DAVIES, S. J., PALMIOTTO, P. A., ASHTON, P. S., LEE, H. S. & LAFRANKIE, J. V. 1998. Comparative ecology of 11 sympatric species of *Macaranga* in Borneo: tree distribution in relation to horizontal and vertical resource heterogeneity. *Journal of Ecology* 86:662–673.

DENSLOW, J. S., NEWELL, E. & ELLISON, A. M. 1991. The effect of understory palms and cyclanths on the growth and survival of *Inga* seedlings. *Biotropica* 23:225–234.

FARRIS-LOPEZ, K., DENSLOW, J. S., MOSER, B. & PASSMORE, H. T. 2004. Influence of a common palm, *Oenocarpus mapora*, on seedling establishment in a tropical moist forest in Panama. *Journal of Tropical Ecology* 20:429–438.

GETIS, A. & FRANKLIN, J. 1987. Second-order neighborhood analysis of mapped point patterns. *Ecology* 68:473–477.

HAASE, P. 1995. Spatial pattern analysis in ecology based on Ripley's K-function: introduction and methods of edge correction. *Journal of Vegetation Science* 6:572–582.

HARMS, K. E., POWERS, J. S. & MONTGOMERY, R. A. 2004. Variation in small sapling density, understory cover, and resource availability in four Neotropical forests. *Biotropica* 36:40–51.

ICKES, K., DEWA LT, S. J. & APPANAH, S. 2001. Effects of native pigs (*Sus scrofa*) on the understorey vegetation in a Malaysian lowland rain forest: an exclosure study. *Journal of Tropical Ecology* 17:191–206.

ICKES, K., DEWALT, S. J. & THOMAS, S. C. 2003. Resprouting of woody saplings following stem snap by wild pigs in a Malaysian rain forest. *Journal of Ecology* 91:222–233.

KOCHUMMEN, K. M., LAFRANKIE, J. V. & MANOKARAN, N. 1990. Floristic composition of Pasoh Forest reserve, a lowland rain forest in Peninsular Malaysia. *Journal of Tropical Forest Science* 3:1–13.

LEVEY, D. J. & BYRNE, M. M. 1993. Complex ant plant interactions – rain-forest ants as secondary dispersers and post-dispersal seed predators. *Ecology* 74::1802–1812.

MANOKARAN, N. & LAFRANKIE, J.V. 1990. Stand structure of Pasoh Forest Reserve, a lowland rain forest in Peninsular Malaysia. *Journal of Tropical Forest Science* 3:14–24.

MANOKARAN, N., LAFRANKIE, J. V., KOCHUMMEN, K. M., QUAH, E. S., KLAHN, J. E., ASHTON, P. S. & HUBBELL, S. P. 1990. *Methodology for the fifty hectare research plot at Pasoh Forest Reserve*. Forest Research Institute Malaysia, Kepong, Malaysia.

MONTGOMERY, R. A. 2004. Effects of understory foliage on patterns of light attenuation near the forest floor. *Biotropica* 36:33–39.

PLOTKIN, J. B., CHAVE, J. & ASHTON, P. S. 2002. Cluster analysis of spatial patterns in Malaysian tree species. *The American Naturalist* 160:629–644.

RIPLEY, B. D. 1976. The second-order analysis of stationary processes. *Journal of Applied Probability* 13:255–266.

SAW LENG GUAN. 1994. *The genus* Licuala *(Arecaceae) in Malaya*. Ph.D. dissertation, University of Reading, U. K.

TAKENAKA, A., TAKAHASHI, K. & KOHYAMA, T. 2001. Optimal leaf display and biomass partitioning for efficient light capture in an understorey palm, *Licuala arbuscula*. *Functional Ecology* 15:660–668.

TIRADO, R. & PUGNAIRE, F. I. 2003. Shrub spatial aggregation and consequences for reproductive success. *Oecologia* 136:296–301.

TURNER, I. M. 2001. *The ecology of trees in the tropical rain forest*. Cambridge University Press, Cambridge. 298 pp.

WALKER, L. R., LODGE, D. J., GUZMÁN-GRAJALES, S. M. & FETCHER, N. 2003. Species-specific seedling responses to hurricane disturbance in a Puerto Rican rain forest. *Biotropica* 35:472–485.

WANG, Y. H. & AUGSPURGER, C. 2004. Dwarf palms and cyclanths strongly reduce Neotropical seedling recruitment. *Oikos* 107:619–633.

WILLS, C. & CONDIT, R. 1999. Similar non-random processes maintain diversity in two tropical rainforests. *Proceedings of the Royal Society of London* 266:1445–1452.