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Short communication

Spatial patterning of *Gonystylus brunnescens* in eastern Borneo

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Abstract

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Determining the spatial patterning of tree species can provide inferences on underlying ecological processes. *Gonystylus brunnescens* is a South-east Asian subcanopy forest tree. To determine the spatial patterns of this species, we recorded the distribution of all individuals in a 0.4 ha sampling plot in eastern Borneo. We found that the pattern deviated from random and was well-described by the Matérn cluster model; clusters had a radius of approximately 4.2 m and contained an average of six seedlings each. This supports the hypothesis of animal-dispersed seeds and, due to a clear lack of association of juveniles with adults, may be due to scatter-hoarding of seeds by small mammal seed dispersers.

Keywords

Kalimantan, ramin, Ripley's K, seed dispersal, spatial clustering, spatial statistics

Introduction

Determining the spatial patterns of plant species is important as it can aid our understanding of ecological processes occurring in a community. For example, the roles of environmental heterogeneity, seed dispersal, disturbance, competition and mortality all are important and can be inferred from the spatial distributions of species. The interactions between adults and juveniles provide key information on the regeneration processes occurring. For example, SEIDLER & PLOTKIN (2006) linked patterns of clustering to the method of seed dispersal in a Malaysian tropical forest and EICHHORN (2010) highlighted small-scale clustering in a boreal *Betula ermanii* Cham. forest attributed to stem suckering. *Gonystylus* (Thymelaeace-ae) is a well-known genus in South-east Asia where there are 32 species with their centre of diversity in Borneo (AIRY SHAW, 1972; SIDIYASA et al., 2010; MANSUR et al. in review) – it is best known for the heavily exploited *Gonystylus bancanus* (Miq.) Kurz that is largely found in

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Fig. 1. (a) *Gonystylus brunnescens* (Thymelaeaceae) studied in the (b) tropical lowland evergreen rain forest at (c) Bukit Bangkirai in eastern Indonesian Borneo.

peat swamp forest (AIRY SHAW, 1972). The majority of the other species have dryland forest distributions and the focus of this paper, Gonystylus brunnescens Airy Shaw, generally grows in lowland forest on typical Ultisols of the region (Figure 1a); it is found in the Malay Peninsula and across Borneo. Gonystylus brunnescens is a sub-canopy species and its fruits are 3.5 to 4.0 cm in diameter and arillate. Although the dispersal agents are not confirmed, birds and mammals are likely dispersers and the similar Gonystylus macrophyllus (Miq.) Airy Shaw is considered to be dispersed by bats (KEVAN & GASKELL, 1986). Whilst there are numerous anecdotal reports of clumped distributions in Gonvstylus species (SHAMSUDDIN, 1996; GRIPPIN et al., 2018), this has rarely been quantified although KOHYAMA et al. (1994) showed clumped distribution of mature (>10 cm dbh) Gonystylus forbesii Gilg trees in Sumatra. There are numerous methods to assess spatial patterns in ecological communities (RIPLEY, 1977; WIEGAND & MOLONEY, 2004; PERRY et al., 2006; LAW et al., 2009; SZMYT, 2014; VELÁZQUEZ et al., 2016) and we use here some commonly applied methods allowing a coarse evaluation of whether patterns are clustered, random or regular that allows us to make comparisons with other studies and hypothesise as to the cause of these patterns.

Materials and methods

Study site

This study was conducted at Bukit Bangkirai (Figure 1b) in East Kalimantan, Indonesia (Figure 1c). Bukit Bangkirai has a mean annual precipitation of 2,000 mm yr⁻¹ and the study plot is found at an elevation of around 110 m in lowland evergreen rain forest. We used the eastern 0.4 ha of a 1 ha plot (Plot K) established by SIMBOLON et al. (2005) (Figure 1b). The 1 ha plot had 445 trees and 141 tree species >10 cm diameter at breast height and was dominated by members of the Dipterocarpaceae as typical for lowland evergreen rain forests of Borneo (BREAR-LEY et al., 2016).

Field observations

In July 2009 we measured the diameter and height, and recorded the co-ordinates of all individuals of *Gonysty-lus brunnescens* in the 0.4 ha plot with a tape measure and reference to marker poles every 10 m × 10 m. These were then categorized into three size classes, namely < 2 cm diameter = 'seedling', 2–< 10 cm diameter = 'pole', >10 cm diameter = 'tree', these were considered to be mature adults. The first two categories were clumped together as 'juveniles' for subsequent analyses.

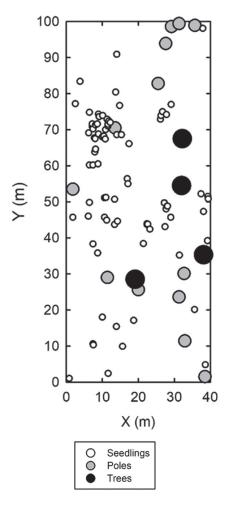
Data analysis

We analysed the pattern of juveniles < 10 cm dbh using spatstat in R (BADDELEY et al., 2015). Spatial patterning was described using the pair correlation function g(r), which is obtained from the first derivative of Ripley's K(r) function (RIPLEY, 1977) and has been applied widely in forest ecology (Law et al., 2009). The pair correlation function shows the density of neighbouring stems at a given distance r from any given stem relative to the spatial average. If densities are independent, then g(r)approximates to 1. We constructed 999 simulations of completely spatially random patterns and compared the observed spatial pattern against the fifth-ranked highest and lowest values of g(r) obtained from random patterns at each distance r. While not a formal test of significance, this is usually interpreted as a two-tailed test ($\alpha \approx 0.01$) (Law et al., 2009). This was evaluated up to 10 m, which is 25% of the minimum dimension of the plot (BADDELEY, et al., 2015). Inspection of graphs allows determination of spatial structures, with values of g(r) greater than 1 indicating that pairs of individuals occur more frequently at a given distance (r) than expected in a random pattern, and g(r) less than 1 that they occur less frequently.

The data were then fit to the MATÉRN (1960) cluster process as an alternative null hypothesis, which simulates a random pattern of cluster centres of intensity κ and distributes a number points drawn from a Poisson distribution of mean σ randomly within a radius *R* from the central points. The three parameters (κ , σ , *R*) were fit by minimum contrast. The effectiveness of this approach in capturing the observed spatial distribution was tested by creating 999 random patterns using a Matérn process with identical parameters and comparing the observed g(r) function with the fifth-ranked values for simulated patterns at each distance r.

Results

In our sampling plot of 0.4 ha, we enumerated 99 individuals of *Gonystylus brunnescens*: 82 seedlings, 13 poles and 4 adult trees (Figures 2 and 3). Within the plot, juveniles (<10 cm dbh) were clustered at scales up to 8.85 m, i.e., there was a greater than random probability of finding a juvenile within 8.85 m of any other given juvenile (Figure 4a). When the data was fit to the Matérn cluster process (Figure 4b), clusters of 4.2 m radius containing a mean of six juveniles were obtained showing good agreement with the scale of clustering as noted above. The expected number of clusters within the plot was 15.6, which was roughly four times the number of adult trees recorded (four); there was no clear visual association between clusters of juveniles and adult trees (Figure 2) although there were too few adult individuals to test this statistically.



Discussion

We demonstrate here that juveniles of Gonystylus brunnescens show a distribution that deviates from random and is well described by a Matérn cluster model indicating a clumped spatial pattern. This agrees with anecdotal information suggesting clumped distributions in other Gonystylus species (SHAMSUDDIN, 1996; GRIPPIN et al., 2018) and concurs with numerous other studies in tropical forests where clustered patterns within species appear to be most common (KOHYAMA et al., 1994; CONDIT et al., 2000; WIEGAND et al., 2009; NGUY-EN et al., 2016; SIREGAR, 2017). Although we did not find any evidence of clustering of juveniles around parent trees, the clustered pattern we found could be due to seed hoarding behaviour (YASUDA et al., 2000) which fits with the suggested dispersal agents of Gonystylus that are small to medium-sized birds and rodents (KEVAN & GASKELL, 1986). This is supported by the work of GETZIN et al. (2014) who found spatial independence between adults and recruits of animal-dispersed species. Thus, animal dispersal is the most likely dispersal method as wind dispersal is not possible for such large seeds and gravity dispersal would result in clustering around parent trees which we did not obviously see. There may also be habitat filtering acting to influence the patterns shown here, but we do not have sufficient additional data on habitat characteristics to test this hypothesis.

Our study differs from many others in that we examined all stems greater than 1 mm in diameter whereas other studies usually examine stems >1 cm dbh (i.e., ForestGEO plots) or larger (CONDIT et al., 2000; WIEGAND et al., 2009; NGUYEN et al., 2016; SIREGAR, 2017). However, the relatively small size of our plot (0.4 ha) restricted the number of individuals of the focal species, and the rectangular shape with a minimum dimension of 40 m limited the analyses as many trees were within close proximity to an edge. It appears that use of the Matérn cluster model is uncommon in spatial analyses of tropical forest trees, but we suggest its use can be explored further as it described our data well.

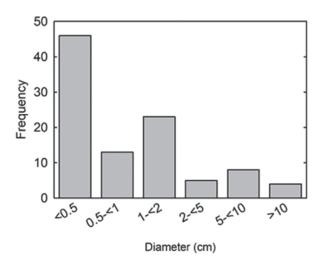


Fig. 2. Spatial distribution of *Gonystylus brunnescens* in three different diameter categories in 0.4 ha (part of plot K) at Bukit Bangkirai, East Kalimantan, Indonesia.

Fig. 3. Number of trees of *Gonystylus brunnescens* in different diameter categories in 0.4 ha (part of plot K) at Bukit Bangkirai, East Kalimantan, Indonesia.

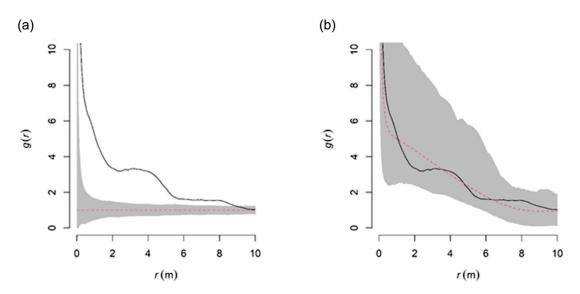


Fig. 4. Spatial clustering of *Gonystylus brunnescens* individuals (<10 cm dbh) in 0.4 ha (part of plot K) at Bukit Bangkirai, East Kalimantan, Indonesia. (a) Compares observed data against a null model of complete spatial randomness; (b) compares data against a Matérn cluster process fitted to the observed pattern. The grey envelope represents the 99% boundary for 999 simulations of a pattern with equal intensity (i.e., the same average density), while the dashed red line shows the null model mean at each distance.

In conclusion, we show that *Gonystylus brunnescens* has a clustered distribution in common with many other tropical tree species and we suggest the pattern we observe here is derived from seed hoarding behaviour of mammal seed dispersers.

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