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Cover Page Footnote

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Population Status and Habitat Preferences of Critically Endangered *Dipterocarpus littoralis* in West Nusakambangan, Indonesia

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Abstract

The conservation of the endemic tree species *Dipterocarpus littoralis* (Bl.) Kurz. is hampered by the paucity of information on its population biology and ecology. Consequently, a targeted survey was carried out in the West Nusakambangan Nature Reserve to assess its population size and structure as well as habitat preferences. In total, 676 individuals of *D. littoralis* were located at 52 locations, with an extent of occurrence of 3.66 km^2 and an area of occupancy of 1.71 km^2. The population had an inverse-J-shaped distribution of diameter at breast height (DBH), with 63% of individuals in the 0-5 cm class and another 21% in the 5-10 cm class; only 11 (1.6%) mature individuals (DBH≥30) were found. *D. littoralis* was associated with steep, low, southwest-facing sites and sites that had high litter cover and thickness. Illegal logging and fuel-wood chopping were the main threats to *D. littoralis* and its habitat. In addition, an invasive shrub, Langkap (*Arenga obtusifolia*, Arecaceae), was a potential competitor with the seedlings throughout the reserve. In view of its endemism, narrow range and localized distribution, small population, environmental preferences, and the severe threats from anthropogenic activities and invasive species, *D. littoralis* appears to more than justify its conservation status of *Critically Endangered*.

Abstrak

Status Populasi dan Preferensi Habitat Jenis Kritis Dipterocarpus Littoralis di Nusakambangan Barat, Indonesia. Usaha konservasi jenis endemik *Dipterocarpus littoralis* (Bl.) Kurz. terhambat karena kurangnya informasi mengenai biologi dan ekologi populasi tumbuhan ini. Oleh karena itu pada penelitian ini dilakukan survey terarah di Cagar Alam Nusakambangan Barat untuk mengetahui struktur dan ukuran populasi serta preferensi habitat dari *D. littoralis*. Total sebanyak 676 individu *D. littoralis* di temukan di 52 lokasi dengan tingkat keberadaan *(extent of occurrence*) 3,66 km^2 dan luas area yang ditempati (*area of occupancy*) 1,71 km^2. Populasi *D. littoralis* memiliki sebaran diameter batang setinggi dada (DBH) berbentuk huruf J terbalik dengan persentase individu dalam kelas DBH 0-5 cm sebesar 63%, kelas 5-10 cm sebesar 21% dan individu dewasa (DBH ≥30) hanya sebesar 1,6%. Keberadaan *D. littoralis* berasosiasi dengan lokasi yang terjal, rendah, menghadap ke tenggara dan memiliki tutupan serta ketebalan serasah yang tinggi. Penebangan dan pengambilan kayu bakar secara liar merupakan ancaman utama terhadap keberadaan *D. littoralis* dan habitatnya. Selain itu, tumbuhan invasif Langkap (*Arenga obtusifolia,* Arecaceae) yang tersebar di seluruh cagar alam merupakan saingan utama anakan *D. littoralis*. Karena bersifat endemik, area sebaran yang sempit dan terlokalisasi, ukuran populasi yang kecil, preferensi terhadap habitat tertentu, dan ancaman yang serius dari aktifitas manusia dan jenis invasif, maka *D. littoralis* memiliki dasar yang kuat untuk tetap dalam status konservasi Kritis (*Critically Endangered*).

Keywords: critically endangered plant, Dipterocarpus littoralis, endemic, habitat preferences, population status

Introduction

Biodiversity is vital to ecosystem stability, human needs, and economic development, yet it has continued to decline over the past decades. The world's plants are the most threatened taxa after amphibians, with one in five plant species threatened with extinction [1]. The main cause of plant species loss is human-induced habitat loss and degradation. Silva *et al*. [2] estimated that habitat destruction is the primary cause of risk for 83% of endangered plant species. The other threats to plant diversity include introductions of alien species, over-exploitation of natural resources, pollution and disease, and climate change [3].

In comparison to those on continents, plants in island ecosystems are more sensitive to the threats as a result of small population sizes and ranges as well as unique characteristics resulting from prolonged evolutionary isolation [4]. According to Sax and Gaines [5], of 80 plant species known to have become extinct in the last 400 years, 50 were island endemics. Moreover, a study by Caujape-Castells *et al*. [6] across nine island groups in tropical and sub-tropical oceanic archipelagos found that single-island endemics are more at risk than multi-island endemics and that this pattern was valid globally. Island endemic plants are also likely to be early casualties of increased temperature caused by global climate change, as they have 'nowhere to go.' Bramwell [7] predicted that a temperature rise of 2-3 °C could result in the extinction of up to half the world's plant species by the end of the century. Therefore, biodiversity conservation strategies and conservation actions need to focus on these vulnerable island endemics.

The giant tree species *Dipterocarpus littoralis* (Bl.) Kurz. is endemic to Nusakambangan Island in Central Java [8]. Predicted to have a distribution range of 80 km^2, it has been categorized as *Critically Endangered* by the International Union for Conservation of Nature (IUCN) since 1998 [9] and included on a national list of priority species for conservation action in Indonesia, 2008-2018 [10]. Ashton [9] stated that illegal logging is a major threat to this species. The trees are illegally harvested despite the presence of two nature reserves and four high-security prisons on the island. Partomiharjo and Prawiroatmojo [11] found only three individuals with a trunk circumference greater than 100 cm (c. 32 cm DBH) during their botanical exploration of the island.

Another potential threat to *D. littoralis* is the expansion in distribution of the Langkap tree (*Arenga obtusifolia*; Arecaceae), a potentially invasive species which is native to Nusakambangan Island. Although it was not a dominant species in 1988 [12], Partomiharjo and Prawiroatmojo [11] suggested that it has come to dominate the vegetation at many locations more recently. This may have a serious impact on the regeneration of *D. littoralis*, especially by competing with young individuals. In the study of Haryanto [12] on the invasion of Langkap in Ujung Kulon National Park, West Java, it was reported that competition for light in areas where Langkap is dominant considerably decreases the relative density of undergrowth and tree seedlings.

To develop a coherent conservation action for a threatened species, basic information on population size and range as well as its habitat requirement are needed. It is also important to assess potential threats to the species or its habitat. No previous detailed habitat assessment or ecological study of *D. littoralis* has been conducted, although a preliminary survey in the West Nusakambangan Nature Reserve was carried out by Kalima in 2006 [13]. This survey estimated density of the tree at 6 ha^{-1} for trunk DBH ≥ 20 cm and c. 1 ha^{-1} for DBH 2-10 cm. The survey could not find any individual with DBH less than 2 cm. The study, however, was lacking information on the location of the surveyed sites and did not mention whether the density was for only the area they surveyed or for the total area of the nature reserve.

The aim of the present study was to assess the population status and habitat preferences of *D. littoralis* in the West Nusakambangan Nature Reserve. The specific objectives were to determine its distribution, population size, and population structure as well as to characterize the environmental conditions associated with established individuals or stands of *D. littoralis*. In addition, we sought to examine the influences of local anthropogenic activities and the potentially adverse effects of the presence of *A. obtusifolia*. Such information would inform assessments of the conservation status of *D. littoralis*, support and facilitate both *in situ* and *ex situ* conservation actions, and provide basic information for the re-introduction and restoration of this species.

Materials and Methods

Study site and species. The study was carried out in the West Nusakambangan Nature Reserve, Nusakambangan Island, Central Java, Indonesia (Figure 1). The reserve was established in 1937 by a decree of the General Governor of the Dutch (No. 34 Staatblad No. 369) and a decree of the Indonesian Minister of Forestry (No. SK.359/Menhut-II/ 2004) to cover an area of 928 ha, located between 7°42'72" S–7°44'50" S and 108°44'04" E–108°47'05" E. The ecosystem is classified as tropical, lowland, evergreen rain forest (Titi Kalima, Pers. Comm. 2011). It provides habitat for several rare and endemic plant species, such as *Rafflesia patma* Blume, *Shorea javanica* Koord. & Valeton, *Hopea sangal* Korth. and *Amorphophallus decus-silvae* Backer & Alderw as well as *Dipterocarpus littoralis* (Bl.) Kurz.

Diptercarpus littoralis (Bl.) Kurz. (Dipterocarpaceae) is a monoecious, emergent tree that grows up to 20-30 m tall. The inflorescences are up to 20 cm long, axillary, and crowded around the twig apices. The fruit is dark red with two long and three short wings. The long wings can be up to 24 cm. The wood is of good quality and is illegally harvested by local people for boat construction, timber, and fuel.

Field survey. The fieldwork was carried out between March 10 and June 25, 2011. Locations were accessed on foot. Searches for *D. littoralis* were conducted by following a footpath located in the middle of the reserve

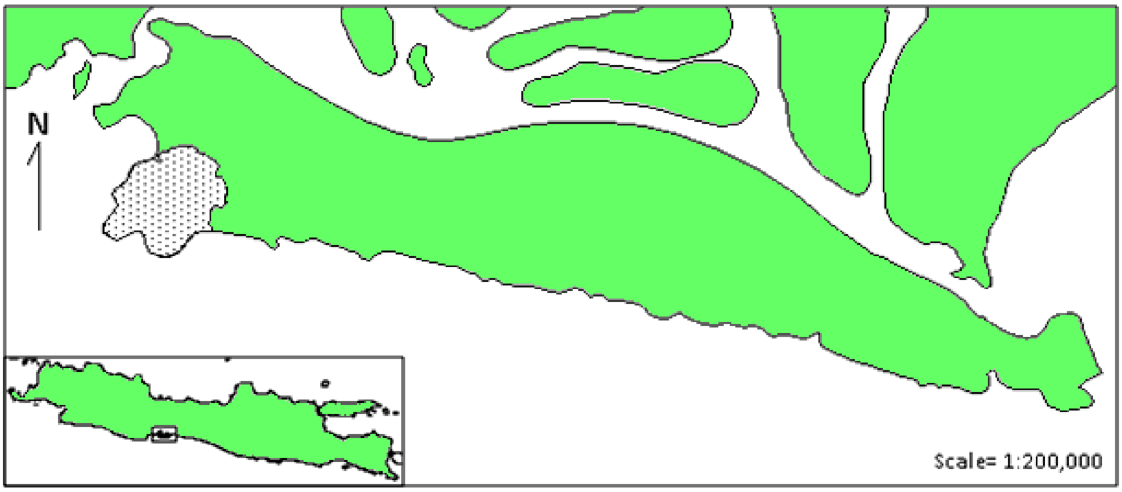

Figure 1. Location of West Nusakambangan Nature Reserve (Dotted Area) in Nusakambangan Island. Small Box in the Inset Shows Location of Nusakambangan Island with Reference to the Java Island, Indonesia

and then creating new paths on either side at right angles to the original path. Where the trees were located, measurements of environmental variables were carried out within 20 m x 20 m quadrats centered on the target tree. The environmental attributes recorded in each center of the quadrat included altitude, slope, aspect, litter thickness and coverage, soil humidity and pH, and the coverage of tree canopy, shrubs and herbs. Altitude, slope, and soil humidity and pH were measured with GPS (Garmin eTrex), an inclinometer, and the Kelway Soil Tester (Kelway HB-2), respectively. The litter, tree, shrub, and herb coverage were estimated using the Daubenmire Cover-Class scale. The location of each quadrat was recorded by GPS.

As most of the trees were found in groups, some of them were not covered by the quadrat. To develop a full population structure and status, all individuals of *D. littoralis* encountered, both inside and outside the quadrats, were recorded and the DBH (DBH=1.3 m) was measured. Individuals with DBH ≥30 were classified as adult trees. Additionally, 150 control 20 x 20 m quadrats were established during the searches in seemingly suitable habitats where *D. littoralis* was absent.

All quadrats were observed for signs of illegal logging, fuel wood cutting, and land cultivation. In addition, the presence/absence of Langkap at each quadrat was recorded, and its coverage was estimated visually using the Daubenmire Cover-Class method.

Distribution and population status. To assess the distribution and population status of *D. littoralis*, all GPS locations for quadrats containing *D. littoralis* were mapped in ArcView, and the ArcView extension Conservation Assessment Tools (CATS) [14] was used to estimate the extent of occurrence (EOO), area of occupancy (AOO), and number of subpopulations. EOO is determined as a minimum convex polygon – a line drawn around all distribution points with no internal angle exceeding 180°. AOO is defined as the area within its EOO that is occupied by the species. Supposing that there is a grid of a set size covering the point distribution, each cell which includes a point is considered an occupied cell. The calculation for AOO is made by multiplying the number of occupied cells by the area of an individual cell. The results were then compared with the threshold set in the IUCN Categories and Criteria Version 3.1, in particular Criterion B1 and B2 for EOO and AOO, respectively [15].

To define subpopulations of *D. littoralis*, CATS used two approaches: Grid Adjacency and Rapoport's Mean Propinquity technique. The first approach considers all contiguous grid cells from the AOO calculations to be one subpopulation, while the latter is based on the mean line length of a minimum spanning tree – that is, a set of lines that connects all points in the minimum possible distance (see [14] for details).

Habitat preferences of *D. littoralis*. To assess the environmental conditions that influence the presence of *D. littoralis*, logistic regression analyses were performed for absence/presence data. All measured environmental variables were used as predictors, with aspect being converted into a dummy variable to simplify the explanation of the results. As this survey was not designed to produce accurate predictive models of species presence, the model was primarily built to indicate which habitat variables might be related to *D. littoralis'* distribution. However, the probabilities of correct classification of presence or absence are shown. The probability cut-off point used to predict presence or absence was 0.5.

For sites with *D. littoralis*, a general linear model (GLM) was used to examine the environmental variables that might influence *D. littoralis* density. All categorical variables – aspect and coverage of litter, tree, shrub and herb – were included as fixed factors. Principal component analysis (PCA) using varimax rotation with Kaiser Normalisation was also used to explore the patterns of presence/absence and density of *D. littoralis* in relation to the environmental variables.

Habitat preferences of Langkap. The influence of environmental conditions on the presence or absence of Langkap were also analyzed using logistic regression analysis and PCA, using all environmental variables measured as independent variables. All analyses were performed using PASW Statistic 18 (SPSS Inc., 2009, www.spss.com).

Results and Discussion

Distribution. *Dipterocapus littoralis* was found at 52 locations, which were generally located in the western part of the reserve (Figure 2). The trees were found in areas with a slope range of 0°-40° and an altitude of 10-108 m. Most of trees were clumped in groups of 1-10 individuals. However, in certain locations, located mostly in the middle of the reserve, the stands could be composed of up to 49 trees. The stands mostly comprised young trees without any adults. There were only six locations with one adult, two with two adults, and two with three adults.

Based on the distribution points of the 52 quadrats containing the trees, the CATS analysis showed that *D. littoralis* has An EOO and an AOO of 3.66 km^2 and 1.71 km^2, respectively (Table 1). According to the IUCN guidelines, this species partly meets several criteria of the *Critically Endangered* category, as the EOO is less than 100 km^2, and the AOO is less than 10 km^2. *D. littoralis* has 10 subpopulations according to the Grid Adjacency approach but only five subpopulations using the Rapoport technique (Table 1).

Population status and structure. There were a total of 676 individuals of *Dipterocarpus littoralis*, only 11 (1.6%) of which were adults (DBH≥30). The population structure of *D. littoralis*, as represented by DBH class, showed a clear inverse-J-shaped distribution (Figure 3). The younger trees dominated the population, as indicated by the very high numbers of individuals in the 0–5 cm (62.6%) and 5–10 cm (20.71%) classes; there was a gradual decrease in the frequency of the intermediate and larger diameter classes.

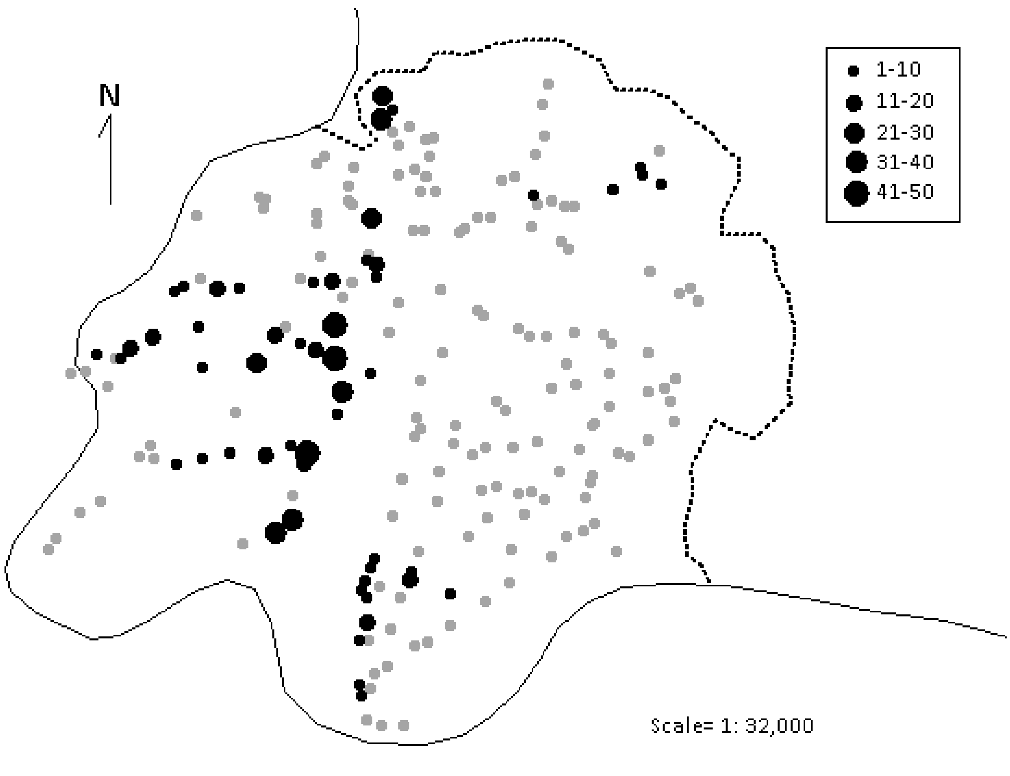

Figure 2. The Distribution of All Sampling Points (Grey Points) and the Quadrats in which *D. littoralis* was Found (Black Points) in West Nusakambangan Nature Reserve. The Size of the Black Points Represents Number of Individuals Found, Inside and Outside the Quadrats

Habitat preferences of *D. littoralis*. The principal components analysis (PCA) of environmental variables extracted five factors, which together explained 65.6% of the variance in the data (Table 2). Factor 1 was characterized by low tree cover and high shrub cover. Factor 2 was characterized by high litter thickness and cover. Factor 3 described non-northern aspect and high soil humidity. Factor 4 described low elevation and high steepness, and Factor 5 was characterized by high soil pH and herb cover. Table 3, however, shows that only Factors 2 and 4 significantly influenced the presence or absence of *D. littoralis***.** PCA highlighted the importance of high litter thickness and cover as well as low elevation and high steepness for *D. littoralis* (Figure 4).

Table 1. The Result of Preliminary IUCN Assessment Using ArcView Extension Conservation Assessment Tools (CATS) based on the Distribution of 52 Quadrats Containing *D. littoralis* (EOO: Extent of Occurrence; AOO: Area of Occupancy)

Measure	Output
Number of collections used	52 consisting of 52 localities
EOO	3.66 km^2 - CRITICALLY ENDANGERED (CR)
AOO: - Cell width/height	0.272348 km
- Number of cells	23
AOO Area	1.71 km^2 - CRITICALLY ENDANGERED (CR)
AOO Subpopulations (Grid Adjacency)	10
Rapoport Subpopulations	5

Table 2. Principal Components Analysis of the Variables Used to Describe Presence of *D. littoralis*. The Loading of Each Environmental Variable on Each Factor is Shown and all Loadings >0.5 are Shown in Bold

Variable	Factor 1	Factor 2	Factor 3	Factor 4	Factor 5
Elevation	-0.09	-0.25	0.28	-0.68	0.03
Slope	-0.12	-0.09	0.30	0.79	-0.03
Aspect	-0.11	0.06	0.73	0.12	-0.01
Soil pH	-0.19	0.11	0.01	-0.15	0.82
Soil humidity	0.14	0.04	0.71	-0.08	0.03
Litter thickness	-0.02	0.69	-0.05	0.17	0.14
Tree cover	-0.86	0.12	-0.01	0.13	0.05
Shrub cover	0.83	0.28	0.01	0.07	-0.03
Herbs cover	0.44	-0.20	0.02	0.2	0.58
Litter cover	0.09	0.78	0.18	-0.08	-0.15
% Variance explained	17.20	13.19	12.37	12.32	10.56

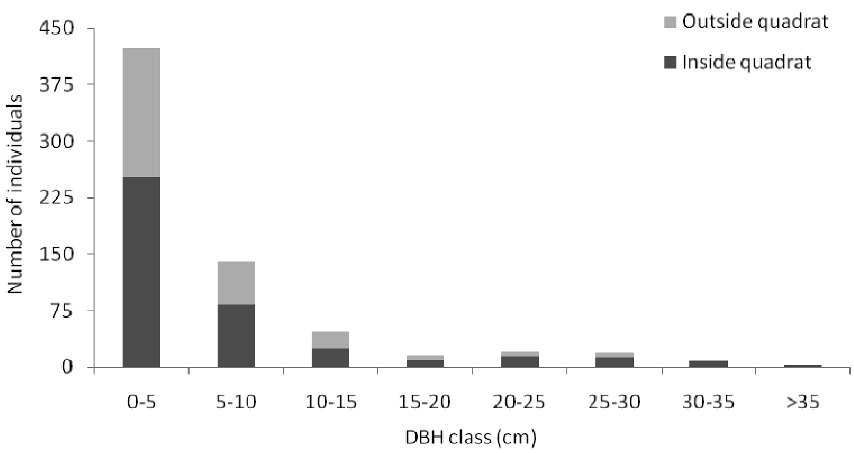

Figure 3. Population structure of *D. littoralis* by DBH class at West Nusakambangan Nature Reserve (*n* = 676)

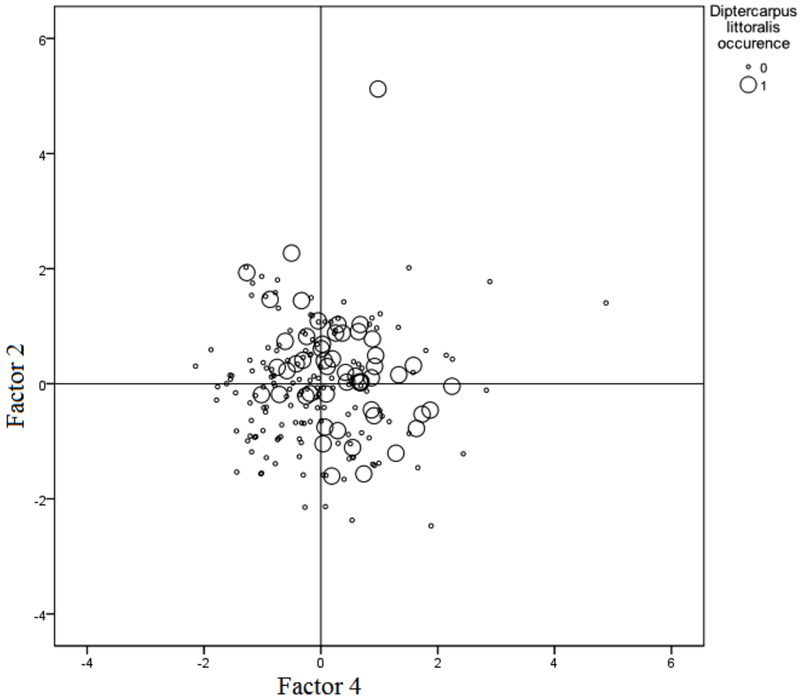

Figure 4. Distribution of *D. littoralis* Occurrence based on Principal Component Factors. Only the Significant Factors are Presented. See Table 2 for Details of Environmental Variables Described by Each Factor and its Explained Variance. The Presence and Absence of *D. littoralis* is Indicated by 1 and 0, Respectively

Table 3. Summary of Univariate Analysis of the Effect of Five Principal Component Factors on the Presence of *D. littoralis*. Significance Levels for F ($^*p < 0.05$, $^{**}p < 0.01$) are Given

Source	df	F
Factor 1	1	0.62
Factor 2	1	5.41*
Factor 3	1	2.44
Factor 4	1	8.91**
Factor 5	1	0.24
Error	196	

Logistic regression analysis indicated that the presence of *D. littoralis* was significantly associated with low-elevation, south-west facing sites (Table 4). The model predicted the absence of *D. littoralis* well but was poor at correctly predicting the presence of the tree. However, this model was generally supported by the result of the PCA analysis.

Where *D. littoralis* was present, the general linear model (GLM) predicted that its density was high at sites with tree cover of 5–25% (Table 5). In this analysis, the five least significant variables (aspect, slope, soil pH, cover of shrubs, and cover of herbs) were excluded from the model to fulfil the minimum of 10 data points per

Table 4. Results of Logistic Regression Analysis of the Environmental Variables Influencing Presence of *D. littoralis*

Environmental variable	Odds ratio
Elevation	-0.02***
Slope	0.04
Aspect : South West	1.31**
Litter thickness	0.17
Litter coverage	ns
Soil humidity	-0.06
Soil pH	-.003
Tree coverage	ns
Shrub coverage	ns
Herb coverage	ns
Overall model Chi-square	23.93***
% Correct presence	21.2
% Correct absence	94
% Correct overall	75.2

Odds ratios, signs (indicating the direction of association) and significance levels ($^*p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$) are given for variables that significantly influenced *D. littoralis* presence. The odds ratios for categorical variables were not shown (ns) as each category within one variable has its own odds ratio value. Regression equation: $P(D)= e^{-0.02E + 1.31S}/(1+ e^{-0.02E + 1.31S})$, where P(D) is the probability of *D. littoralis* is present in any site, E is elevation and S is south west aspect.

predictor. Further, PCA identified five factors that together explained 71.6 % of the variance in the data (Table 6) but detected no environmental variables influencing tree density (Table 7).

Habitat degradation. Several indications of habitat degradation in the West Nusakambangan Nature Reserve were observed during the study. Illegal logging by local people was the most commonly found activity. Benda *(Artocarpus elasticus*, Moraceae) and *D. littoralis* were two tree species usually cut down for home construction, building boats, or fuel wood (Figure 5a, b, and c). The signs of logging activities were generally observed in forest areas near the beach, where the wood can be easily transported using boats. Besides illegal logging, land cultivation was also a potential threat for the reserve. Several areas that have clearly been used as farmland and which are now fully covered by shrubs were found within the reserve. We also encountered many banana, cassava, and other commodity plantations located near the border of the reserve (Figure 5d).

This study was the first detailed survey of *D. littoralis* ecology in the West Nusakambangan Nature Reserve. Since it was a targeted survey of one rare, endemic species, relatively few sampling points were placed in areas where the species was absent. The 52 locations where the trees were found represent a considerable increase in the known records, based on studies of herbarium specimens in Kew Herbarium, where only four localities had been recorded.

The distinctive, clumped spatial distribution among tropical tree species is well-established [16–17]. Bunyvejchewin *et al*. [18] suggested that the cause of this pattern might be poor dispersal of propagules, leading to high densities of seeds and seedlings directly below the crown of a mother tree and an exponential decrease with distance from the mother tree. In the current study, most young *D. littoralis* were clumped, but only at 11 locations were the stands in close proximity to surviving adults. The absence of the adults from most of the localities might be due to illegal logging, as there was no evidence of dead adults.

Rather, stumps of *D. littoralis* were encountered at several locations. Hubbell [19] hypothesized that having highly clumped populations was one way that a rare species could persist, as a strategy to ensure effective pollination and increase the probability that a viable seed will fall in a suitable habitat.

Several studies (e.g., [19–20]) have related the clumping of juveniles of tree species near to conspecific adults to seed source and resource patchiness. Despite having two long wings, the seed of *D. littoralis* might have poor dispersal ability. Where there is closed-canopy cover, dipterocarp fruits generally disperse short distances, usually no more than 60–80 m [21]. The study by Takeuchi *et al*. [22] on the sapling demography of *D. globosus* and *D. tempehes*, which also have two long wings on their seeds, found that the saplings (DBH≤10) of these two species were strongly concentrated near mature trees, although some of the saplings could be found more than 30 m away from conspecific adults. The occurrence of juveniles is also related to resource patches. Suitable light conditions and water availability

Table 5. Results of General Linear Model of the Environmental Variables Influencing the Density of *D. littoralis*. F Values, beta Coefficient of Parameter Estimates for Significant Variable and Significance Levels (*p < 0.05 are Given)

Source	Df	F	B
Elevation	1	2.89	
Litter thickness	1	2.10	
Litter coverage	3	1.96	
Soil humidity	1	0.74	
Tree coverage	4	3.40^{*}	$10.14^{*(a)}$
Error	41		

R^2=0.34; (a) Only B value for tree coverage of 5-25% was significant

Table 6. Component Matrix from a Principal Components Analysis of the Variables Use to Describe the Density of *D. littoralis*. The Loading of Each Environmental Variable on Each Factor is Shown and all Loadings >0.5 are Shown in Bold

Variable	Factor 1	Factor 2	Factor 3	Factor 4	Factor 5
Elevation	0.21	-0.45	0.52	-0.28	0.34
Slope	0.72	-0.06	-0.19	0.13	-0.08
Aspect	0.42	-0.61	-0.08	0.41	0.17
Soil pH	0.14	0.79	0.01	0.08	0.11
Soil humidity	-0.05	0.04	0.21	0.90	0.11
Litter thickness	-0.12	0.06	-0.05	0.12	0.89
Tree cover	-0.57	0.39	0.41	0.14	0.08
Shrub cover	-0.68	0.14	-0.22	0.26	-0.25
Herbs cover	-0.67	-0.11	-0.03	0.10	0.29
Litter cover	-0.06	0.07	0.87	0.27	-0.13
% Variance explained	20.11	14.11	13.22	12.70	11.48

Table 7. Summary of Univariate Analysis of the Effect of Five Principal Component Factors on the Density of *D. littoralis*. Significance Levels for F (*p < 0.05, **p < 0.01, ***p < 0.001) are Given

Source	df	F
Factor 1	1	0.93
Factor 2	1	0.004
Factor 3	1	1.46
Factor 4	1	0.06
Factor 5	1	0.002
Error	46	

Figure 5. General View Of Habitat Degradations that Threaten West Nusakambangan Nature Reserve. a. Benda Tree (*Artocarpus elasticus*, Moraceae) that has Fallen Down as a Result of Chain Saw Cutting; b. The Basal Part of *D. littoralis* that Remains Standing After the Tree has been Felled; c. The Wood of Benda Tree Ready for Shipping; d. A Banana Plantation Located Near the Border of the Reserve

in this habitat are more likely to occur near the adults, as will be discussed below. Both of these two processes might have contributed to the strong clumping of *D. littoralis*, at least as judged by visual observation; further quantitative study of the spatial distribution pattern is desirable to confirm this.

This study showed that *D. littoralis* comprised five to ten subpopulations, depending on the method used – an EOO of 3.66 km^2 and an AOO of 1.71 km^2. Under the IUCN guidelines, *D. littoralis* meets, in part, *Critically Endangered* category criteria B1 and B2. To fulfil all the criteria of this category, data on population trends that show a continuing decline would be required; these could be obtained only by longer-term fieldwork. In addition, criterion D for the category can also be applied, since there were only 11 mature trees of the species – fewer than the threshold of 50 set in the criteria. This, however, requires caution, as the definition of maturity used (DBH ≥ 30 m) was based on studies of other dipterocarp species [22–23] because no flowering tree was observed during the survey. Thus, the number of mature individuals could be lower or higher than 11. Further study of the flowering and reproductive biology is clearly needed.

The population structure of *D. littoralis* had a inverse-J-shaped pattern. This distribution is common for most dipterocarp species that have a high density of young, relatively shade-tolerant individuals [24].

Such a structure is often regarded as characteristic of a healthy or expanding population, where individuals are naturally replacing themselves with continuous recruitment [25–27]. In the case of *D. littoralis*, however, it is also more likely to be caused by the illegal logging of individuals with high DBH, depleting the number of mature individuals observed in the reserve.

According to the PCA, thick litter cover, low elevation, and steep slopes were associated with the presence of *D. littoralis*. Logistic regression also implicated low elevation and south–west facing aspect as factors in its niche. Most of the litter layer, however, was derived from old leaves of *D. littoralis,* and so the association is more likely an effect of *D. littoralis* presence than a determinant of it. Low elevation and steep slopes are features found along the small streams near to the water table, indicating that water availability may be one of determinants of establishment of *D. littoralis*, even though soil moisture was not significant in the models. This might also be manifested in its preference for south–west facing sites. Studies by Hedberg [28] on Mt. Meru (Tanzania, latitude 3º S) and Smith [29] on Fiji Island (latitude 15–20º S) also featured forest formation on the wetter southerly slopes. Furthermore, Barry [30] in New Guinea (latitude 6º S) noted significant differences in mean humidity and temperature between east- and west-facing slopes, because of high radiative fluxes on east-facing slopes during the early morning.

The density of *D. littoralis* was predicted to be high at sites with tree canopy cover of only 5–25%, characteristic of the larger gaps in the forest. As there were indications of shade-tolerance from its population structure, *D. littoralis* seems to fit Whitmore's [31] definition of a climax species with low shade tolerance: able to germinate and establish beneath the closed canopy but requiring large gaps to successfully recruit into the canopy layer. Since the population is dominated by young individuals, all the environmental associations revealed by this study might be related to the regeneration stage of the life cycle rather than the growth of established trees. This needs to be taken into consideration for both *in situ* and *ex situ* conservation plans for *D. littoralis* and especially when reintroducing the seedling or seeds to its native habitat, or when propagating or planting the trees as an *ex situ* conservation action.

The main cause of plant extinction around the globe is habitat fragmentation and disturbance [32]. In the case of *D. littoralis*, illegal logging and fuel wood chopping are prominent and major causes of disturbance and the destruction of its habitat. Local people from areas around the reserve are the main culprits. Their activities increase when income from fishing is low, as the majority of local people are fishermen. Another threat to the habitat of *D. littoralis* are the plantations located near the border of the reserve. Since the West Nusakambangan Nature Reserve is managed by only one person, there is a serious danger that weak monitoring and law enforcement may allow the plantations to cross the border and encroach on the reserve.

Invasive species are widely considered to be the second greatest cause of species endangerment and extinction globally [33]. Langkap (*Arenga obtusifolia)*, known as a native to Nusakambangan Island [12], was found widely distributed across the West Nusakambangan Nature Reserve. This tree could be regarded as a habitat generalist, since it showed no preferences for any environmental variables that we measured. This agrees with the multispecies metapopulation analysis of Marvier *et al*. [34], which showed that invasive species tend to exhibit habitat preferences that are broad relative to those of closely related non-invasive species. On average, Langkap cover was 25–50 % in the quadrats. This would have been detrimental to *D. littoralis*, since a canopy cover of 5–25% proved important for its density. According to Prayitno [35] the density of seedlings and saplings of other plant species is low in areas where Langkap is dominant. This phenomenon is closely related to poor light under the Langkap canopy, as less than 5% of the light reaches the forest floor [36]. The effect could be serious in the longer term, because of the stability of Langkap regeneration. Muntasib and Haryanto [37] reported that the regeneration of Langkap is particularly promoted by its capacity for rapid recovery after the destruction of the above-ground parts from subterranean shoots, high fecundity (one tree can produce 945–5400 seeds per fruiting spadix), and ability to defend against herbivores. The immature seeds of Langkap contain toxic concentrations of oxalates, which deter herbivores [38]. This is advantageous to Langkap since the herbivores prefer to eat the mature seeds that are ready for germination.

This study was not able to survey areas outside the West Nusakambangan Nature Reserve. Since it is reported to be restricted only to Nusakambangan Island [17], the possibility that *D. littoralis* is present outside the nature reserve still exists. The land use on the island, however, renders this unlikely. Most areas on the island are unprotected and open to farming for local people. Apart from this, illegal logging, the presence of the prisons, and the concomitant social activities of their inmates, as well as legal limestone mining located in the eastern part of the Island, all militate against the survival of *D. littoralis*. Thus, the West Nusakambangan Nature Reserve is probably the only place where *D. littoralis* can survive, and, therefore, the protection of the reserve and its habitat is key to conserving this tree.

This study suggests that *D. littoralis* justifies its conservation status of *Critically Endangered*. Recommendations for its conservation include the following: a). Establishing permanent plots in all subpopulations of *D. littoralis* so that they can be monitored for signs of declining population. These plots would also be important for investigating its reproductive biology; b). Controlling Langkap. Mechanical clearance by cutting is known to be effective in increasing the diversity of other seedlings and saplings; c). Adding *D. littoralis* to living collections in botanic gardens. Currently, live specimens are represented only in Bogor Botanic Garden, which holds two collections of *D. littoralis*; d). Preserving seeds in local seed banks and distributing them to other regional conservation organizations. Designing, initiating, and establishing protocols for *in vitro* conservation; e). Minimizing the anthropogenic activities within the reserve (especially illegal logging and fuel wood cutting); f). Increasing the security at the border of the reserve and strict law enforcement to prevent the plantations from encroaching on the reserve; g). Creating alternative, environmentally sustainable employment for the local inhabitants, especially in periods of low fishing catches.

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