BIOTROPICA
THE JOURNAL OF TROPICAL BIOLOGY AND CONSERVATION

A Conservation Assessment of Dipterocarps in Sabah: Comparison of Methods and Future Prospects

Journal:	*Biotropica*
Manuscript ID:	Draft
Manuscript Type:	Paper
Keywords:	Dipterocarpaceae, ecological niche modelling, IUCN Red List, regional Red List, threatened tropical tree species

A Conservation Assessment of Dipterocarps in Sabah: Comparison of Methods and Future Prospects

LRH: Maycock *et al.*

RRH: Conservation Assessment of Dipterocarps

Colin R. Maycock[1,3,5], Eyen Khoo[1], Chris J. Kettle[2], Joan T. Pereira[1], John B. Sugau[1], Reuben Nilus[1], Robert C. Ong[1], Nazahatul Anis Amaludin[3], Mark F. Newman[4] & David F.R.P. Burslem[3]

[1] Forest Research Centre, Sabah Forest Department, Sandakan 90715, Sabah, Malaysia

[2] Institute of Terrestrial Ecosystems, ETH Zürich, CHN G 73.1, Universitätstrasse 16, Zürich 8092, Switzerland

[3] Institute of Biological and Environmental Sciences, University of Aberdeen, Cruickshank Building, St Machar Drive, Aberdeen, AB24 3UU, UK

[4] Royal Botanic Garden Edinburgh, 20A Inverleith Row, Edinburgh EH3 5LR, UK

[5] Corresponding author; e-mail: soi530@abdn.ac.uk

Received________; revision accepted______.

ABSTRACT

Sabah has experienced a rapid decline in the extent of its natural forests. This reduction in forest cover is reducing the amount of habitat available for many species, but the precise impacts of habitat loss on the conservation status of dipterocarps is uncertain. We use three contrasting techniques, the extent of occurrence (EOO), area of occupancy (AOO) and ecological niche models derived using MAXENT, to reconstruct historic distributions for 33 dipterocarp species. We compare these maps to the current distribution of forest cover to derive estimates of habitat loss and infer a conservation status using the IUCN red list categories for the Sabah populations of these species. Estimates of habitat loss differed significantly among the different techniques and between species of different habitat types. Predicted habitat loss determined from the ecological niche models varied from 21 percent for *Shorea micans* to 99.5 percent for *Dipterocarpus lamellatus*, and 32 of the 33 dipterocarp species analysed in this study (97%) would have their Sabah populations classified as Threatened under the A2 criteria. Dipterocarps that occur in lowland forests have experienced a greater proportional habitat loss than upland/lower montane or ultramafic species. In addition, species with the lowest predicted area within their historic distributions had the highest proportion of habitat lost, which provides a basis for targeting conservation effort on the species with narrow distributions. We recommend the ecological niche modelling approach as a rapid assessment tool for reconstructing species' historic distribution during conservation assessments of tropical trees.

Key words: Dipterocarpaceae; ecological niche modelling; IUCN Red List; regional Red List; threatened tropical tree species.

THE GLOBAL STRATEGY FOR PLANT CONSERVATION MAKES CLEAR THAT HALTING THE DECLINE of plant diversity is one of the greatest challenges facing the global community (Secretariat of the Convention on Biological Diversity 2002). Nowhere is this more urgent than in the forests of Southeast Asia, which have the greatest proportion of threatened vascular plant species in the tropics and the highest annual rates of deforestation (Sodhi *et al.* 2010). This rapid and on-going loss of forest is one of the many causes of the international failure to meet the 2010 Biodiversity Targets established by the Convention on Biological Diversity (Asia Pacific Forestry Commission 2010).

In the Malaysian state of Sabah there has been a rapid decline in the extent of the natural forests, from about 86 percent in 1953 to less than 50 percent currently (McMorrow & Talip 2001, Sabah Forestry Department unpubl. data). This decline is disproportionately high in the lowland coastal regions, particularly around the west and north coasts of Sabah, and has varied among the different forests types represented in the state (Table S1). This reduction in forest cover is leading directly to the endangerment, and local extinction, of many plant and animal species (Sodhi *et al.* 2010), which may include dipterocarps. It is not possible currently to determine the impact of this habitat loss on the conservation status of most species in Sabah, as there have been no attempts to reconstruct historic species distributions prior to the recent losses of forest cover. In this paper we use three contrasting techniques to reconstruct these historic distributions for 33 dipterocarp species and compare these maps to the current distribution of forest cover. We use these comparisons to infer conservation assessments of the Sabah populations of the 33 dipterocarp species and contrast our assessments to those derived by other authors using different methods.

Despite the importance of plant community diversity for maintaining ecosystem function (Naeem *et al.* 2009, Scherber 2010), plant species receive relatively little conservation effort compared to the more charismatic mega fauna (Ashton 2008). In Sabah, there is currently little emphasis on the conservation of individual plant species, which reflects a lack of information about their conservation status (Ministry of Science, Technology and the Environment 1998). This emphasis may change following the creation of the Aichi targets during the recent COP 10 meeting of the Convention on Biological Diversity. Target 12 calls for the development of national red lists and conservation strategies for threatened species (Secretariat of the Convention on Biological Diversity 2010). Similarly, Target 2 of Malaysia's National Strategy for Plant Conservation aims to have preliminary assessments of the conservation status of all known plant species in Malaysia (Chua *et al.* 2010). These regional red lists will permit the identification of priority species for conservation action (Fitzpatrick *et al.* 2007).

One of the problems faced by regions rich in biodiversity, such as Borneo, is that the number of experts available to conduct the assessments is low relative to the amount of work required. Sabah alone has more than 8000 plant species and it would be impractical to conduct detailed assessments of all these species within a reasonable period of time. Therefore alternative assessment strategies that are cost effective and feasible are needed to inform conservation decision making. Estimating the extent of a species' distribution by measuring its extent of occurrence (EOO) or area of occupancy (AOO) are two commonly used approaches (Chua *et al.* 2010). The EOO is defined as the area contained within a polygon drawn to create the shortest boundary solution encompassing all known sites of occurrence of a species, while the AOO measures the area within the extent of occurrence that is actually occupied by a given species (IUCN Standards and Petitions Subcommittee 2010). The AOO is determined by counting the number of occupied cells in a uniform grid covering the species range and then multiplying the number of occupied cells by the size of the grid cell adopted (IUCN Standards and Petitions Subcommittee 2010). This approach may be a suitable measure of range-restricted species (Brummitt *et al.* 2008), but for the majority of plants it needs to be coupled with estimates of habitat loss (McIntyre 1992, Nic Lughadha *et al*. 2005) and population size (Brummitt *et al.* 2008) in order to provide meaningful conservation assessments.

Estimating the extent of a species' distribution and subsequently its loss of habitat is not straightforward, as most tropical plants are known from only a few collections and are often highly habitat-specific (Ashton 2004, Cannon & Leighton 2004, Davis *et al.* 2005). In Borneo, habitat associations are particularly common among dipterocarps, as many species display a strong degree of specificity to soil type (Paoli *et al.* 2006, Sukri *et al.*, in press) and they are often naturally fragmented into an archipelago of habitat islands (Ashton 2004, 2010). Ashton (2004, 2008) considers that the IUCN assessment criteria may not be suitable for assessing the conservation status of these long-lived, highly habitat specific trees, a view which is supported by previous work showing that neither the EOO nor the AOO is effective for estimating distributions of species with disjunct distributions (Solano & Feria 2007). The extent of occurrence (EOO) over-estimates the distribution of species with disjunct distributions because it fails to account for the patchy distribution of habitat (Solano & Feria 2007), while use of the AOO can lead to under-estimation of species distributions because of sampling constraints (Solano & Feria 2007). A new and alternative solution is to use ecological niche modelling as a cost effective means of estimating the potential distribution of threatened species where distribution data are lacking or difficult to collect (Irfan-Ullah *et al.* 2007, Solano & Feria 2007). These approaches use algorithms to generate maps of a species' potential distribution on the basis of a mathematical representation of its distribution in environmental space (Phillips *et al.* 2006). Numerous techniques for generating ENMs have been proposed (Elith *et al.* 2006), and the relative merits of the different techniques are debated (Elith *et al.* 2006, Graham *et al.* 2008). In this paper we use the program MAXENT for modelling the distributions of 33 dipterocarp species in Sabah (Phillips *et al.* 2006). Because this method explicitly incorporates the strong habitat associations of dipterocarps, we predicted that it would generate lower estimates of range size than alternative methods that fail to capture this important element of dipterocarp ecology. This over-estimation of range size may lead to an under-estimation of percent habitat loss and ultimately lead to inappropriate conservation assessments.

The ecological dominance, and commercial importance, of the Dipterocarpaceae in the forests of Southeast Asia has stimulated a significant quantity of ecological and taxonomic research on the family (Ashton 2004, 2008, 2010). As a result, dipterocarps are the most well-studied component of the flora of Borneo, and serve as an appropriate model for developing and testing rapid assessment strategies. Approximately 58 percent of all dipterocarps have been evaluated for the IUCN Red List, of which 94 percent are listed as endangered (Nic Lughadha *et al.* 2005), although there is uncertainty over the accuracy of these assessments (Chen 2004). In this study we compared estimates of habitat loss based on reductions in the extent of occurrence, area of occupancy and predicted distributions determined by ecological niche modelling for 33 dipterocarp species in Sabah. Based on these estimates of habitat loss, we classified the Sabah populations of each species into a threat category based on the A2 criterion (IUCN Standards and Petitions Subcommittee 2010), and these threat assessments were compared with previous assessments that were implemented using the extent of a species geographical range (Criterion B; Chua *et al.* 2010) and non-quantitative expert assessments (Ashton 2004, IUCN 2010). We also use the species distributions predicted using MAXENT and estimates of habitat loss to test the hypothesis that habitat loss is more significant, as a proportion of total habitat area, for range-restricted and/or habitat-specialist species.

METHODS

Ecological niche models were generated for the 33 dipterocarp species using MAXENT v. 3.3.1 (www.cs.princeton.edu/~schapire/maxent/, Phillips *et al.* 2006) based on locality data obtained from herbarium specimens, current research plots and field surveys (Table S2). MAXENT has been shown to outperform other modelling techniques (Elith *et al.* 2006) in the sense that it is least affected by errors in locality data and gives more robust outcomes when there are few collection localities (Graham *et al.* 2006, Wisz *et al.* 2008). This method uses maximum entropy density estimations to represent the distribution of a species as a probability distribution over the study area (Phillips & Dudík 2008). The models are derived from locality data (presence-only data) and a set of environmental variables that are considered the most important for defining the suitability of the environment for the species. These data are used to develop a model that predicts environmental suitability as a function of the environmental variables. The model is then projected into geographic space to predict the distribution for the species (Phillips *et al.* 2006). Model validation is conducted by testing the prediction success of the model on an independent data-set (Cayuela *et al.* 2009).

Collection locality data were sourced from herbarium specimen labels held in the Sandakan herbarium. All herbarium specimen locality records without geographical coordinates were geo-referenced by consulting 1:250,000 soil maps and 1:50,000 forest stratum maps.

Samples that could not be placed confidently were excluded from the study to avoid the use of imprecise distributional information. Supplementary locality data were collected from research plots and during field surveys (Sabah Forestry Department, unpubl. data). All dipterocarps encountered during these surveys were identified and their position recorded with a GPS (Garmin GPSmap CSX60). Where multiple samples/records had been collected from the same soil type in one locality (corresponding to a 2 x 2 km grid cell on a map of Sabah), only one sample was included in the analysis to reduce sampling bias (Hijmans *et al.* 2000). Conversely, collections from more than one soil type within a 2 x 2 km grid cell were included as independent items of data for constructing species distributions.

The ecological niche models were developed using bioclimatic, altitudinal and edaphic variables. Bioclimatic data for Sabah at 30 arc seconds (~1 km^2) resolution were obtained from WorldClim (www.worldclim.org). Shuttle Mission Radio Telemetry altitudinal data at three arc-second resolution (~ 90 by 90 m) were obtained from the CGIAR-CSI GeoPortal (srtm.csi.cgiar.org). The slope of the terrain was calculated from the altitudinal data using ArcView 3.3. GIS shapefiles of soil association, landform, soil suitability and soil parent material were obtained from the Sabah Forestry Department (Sabah Forestry Department, unpubl. data). The shapefiles were converted to ESRI ASCII grid format using ArcView Spatial Analyst. All spatial data were on the WGS84 projection. As the edaphic variables are categorical and cannot be aggregated into larger mapping units, it was necessary to set the grid size to the smallest common size of 6 arc seconds (~ 0.04 km^2).

For the 20 species with more than 12 collecting localities we ran two separate models. The first model was developed using the full set of locality data to provide best estimates of the species' potential distributions for interpretation, and the second model was developed using a random selection of 75 percent of the locality data at each iteration as a training data-set, with the remaining 25 percent reserved for testing the resulting model. For species with fewer than 12 collection localities no model testing was conducted. The area under the curve (AUC) of the receiver operating characteristic (ROC) for each model testing run is given in Table S2. In all cases, we ran 100 replicated runs of MAXENT on the locality data with 10,000 background points randomly selected per run (Phillips *et al*. 2006).

We used DIVA-GIS 7.1.1.1 to estimate the percentage of habitat loss for each species (Hijmans *et al.* 2005). The average predicted distribution from 100 replicated runs of MAXENT was used as an estimate of the total historic distribution of each species. This distribution map was overlaid with a grid file showing the current land-use in Sabah in 2008 (Sabah Forestry Department, unpubl. data), which enabled us to calculate the percent of the historic distribution that currently falls into protected areas, production forests under natural forest management or in land that has been, or is currently, being converted to alternative land-uses. Habitat loss was calculated as the historic distribution minus the area retained in protected areas or production forests. This approach assumes that no extant populations of the species exist outside the permanent forest estate, and that all protected areas and production forests under natural forest management still maintain populations of the study species. The validity of these assumptions is discussed below. Species were classified into threat categories based on the percent of habitat loss using the A2 criterion (IUCN Standards and Petitions Subcommittee 2010). Criterion A is designed to highlight species that have undergone a significant decline, measured either as a decline in population size or habitat area, in the recent past or are projected to experience a significant decline in the near future. This criterion is more relevant for a regional assessment than Criterion B, which is the size of the geographic range of a species. While Criterion B is meant to be a reliable indicator of the extinction risk of a species, there are concerns over its validity when applied at a regional scale (Abeli *et al.* 2009). Our approach also assumes that all loss of forest cover has occurred within three generations of the study species. We selected the A2 criterion as the habitat/population reduction has neither ceased nor is reversible in the majority of cases.

All locality data were used to determine the extent of occurrence (EOO) and area of occupancy (AOO). The extent of occurrence is a measure of the spatial spread of the area occupied by the species and is not intended to be an estimate of the amount of potential habitat or range size (IUCN Standards and Petitions Subcommittee 2010). EOO was calculated by the minimum convex polygon method using the Conservation Assessment Tools CATS produced by the Royal Botanic Gardens Kew (Moat 2007), and includes discontinuities in habitat (Gaston & Fuller 2009). The area of occupancy was calculated using CATS based on a 2 x 2 km grid cell as recommended by the IUCN Standards and Petitions Subcommittee (2010). Habitat loss as a percentage of EOO was calculated using DIVA-GIS 7.1.1.1 by converting the EOO polygon to a grid file, overlaying the current land-use grid file, and calculating the percentage of EOO outside protected areas and the permanent forest estate (Hijmans *et al.* 2005). While this does not conform to the IUCN Standards and Petitions Subcommittee (2010) recommended practice for determining a reduction in EOO, it was the only approach that was possible with the available data. Habitat loss based on a reduction in AOO was calculated using the herbarium collections only following Callmander *et al.* (2007).

The species were classified as lowland, largely ultramafic or upland/montane based on Ashton (2004), to allow comparison between species occupying different habitats. ANOVA was used to test the significance of differences in percent habitat loss among species occupying these three habitat types and among the different assessment methods using transformed percent habitat loss data. Linear regression models were used to investigate the relationship between habitat loss and distribution area predicted from the AOO, EOO and ecological niche models. Finally, to allow comparison between this work and previous assessments (Ashton 2004, Chua *et al.* 2010, IUCN 2010), we assigned a numeric value from 0 to 5 to each threat category, with 0 corresponding to an assessment of 'least concern' and 5 being 'extinct'. Paired Wilcoxon tests were used to test for a difference in median scores between the assessments. All analyses were conducted using R 2.12.0 (R Development Core Team 2010).

RESULTS

COMPARISON OF ASSESSMENT METHODS AND HABITAT TYPES.—Predicted habitat loss determined from the ecological niche models varied from 21 percent for *Shorea micans* to 99.5 percent for *Dipterocarpus lamellatus*, with 32 of the 33 dipterocarp species analysed in this study (97%) classified as threatened (equal to a habitat loss of > 30%) under the A2 criteria (Fig. 1a). Mean (± SEM) habitat loss for the six upland/montane and ultramafic species (37.6 ± 5.7 %) was significantly lower than for the 27 lowland (68.6 ± 2.3 %) species ($F_{2,30}$ = 13.3, P < 0.0001). Among the lowland species, the proportion of the habitat lost was greatest in species with the lowest predicted area within the historic distribution (Fig. 1a, $R^2_{adj.}$ = 0.57, P < 0.0001).

Estimated habitat loss calculated from reduction in EOO ranged from 39 to 74 percent, and all 33 dipterocarp species were classified as threatened (VU or EN: Fig. 1b). We found no significant difference in percentage habitat loss among species of lowland, ultramafic or upland/montane environments ($F_{2,29}$ = 1.74, P = 0.192, Fig. 1b), and no significant relationship between the EOO of the lowland species and the proportion of habitat lost ($R^2_{adj.}$ = 0.016, P = 0.534). By contrast, only 63 percent of the species examined were classified as threatened based on reduction in AOO (Fig. 1 c), and there were no significant differences in estimated habitat loss between species of lowland, upland/montane and ultramafic environments ($F_{2,\mathbf{30}}$ = 2.164, P = 0.132). For the lowland species, there was a significant negative relationship between AOO and the proportion of habitat loss based on reduction in AOO (Fig. 1c, $R^2_{adj.}$ = 0.36, P = 0.0006).

Estimates of habitat loss differed significantly according to whether historic distributions were estimated using EOO, AOO or ecological niche models ($F_{2,89}$ = 18.41, P < 0.0001) and between species of different habitat types ($F_{2,89}$ = 9.92, P = 0.0001). The interaction between computational method and habitat types was also significant ($F_{4,89}$ = 3.71, P = 0.0076, Fig. 2). For lowland forest species, estimated habitat loss was higher when based on ecological niche models (mean ± SEM: 68.6 ± 2.3 %) than either reduction in AOO (mean ± SEM: 44.8 ± 4.2 %) or EOO (mean ± SEM: 52.1 ± 1.4 %). For ultramafic and upland/montane species the method based on reduction in EOO estimated highest habitat loss (Fig. 2a & 2c). There was closer agreement in the threat categories obtained when comparing between the methods based on ENMs and reduction in either the EOO or AOO (Fig. 2a & 2 b), than when comparing between the methods based on reduction in EOO and AOO (Fig. 2c).

COMPARISONS WITH PREVIOUS ASSESSMENTS.—There were significant differences in the distribution of species among categories of threat based on the six assessments available for comparison: those based on the three methods adopted in our study, the current global assessments (IUCN 2010), the Malaysia Plant Red List project assessments (Chua *et al.* 2010) and Ashton's (2004) assessments (Table 1). Of the 23 species examined in this study that were also assessed for the IUCN Red List, 20 species had a higher global threat category on the IUCN Red List (Table 1). By contrast, all 11 species examined by Chua *et al.* (2010) for the Malaysia Plant Red List had lower threat categories on the Malaysia Plant Red List. We found no significant differences between our assessments based on EOO and ENMs and Ashton's (2004) assessments based on expert opinion (Table 2), but Ashton's (2004) assessments were significantly lower than the global assessments (IUCN 2010) and significantly higher than the Malaysia Plant Red list project assessments (Table 1).

DISCUSSION

COMPARISON OF METHODS FOR COMPUTING HABITAT LOSS.—Our estimates of percent loss of habitat within species' historic distributions varied significantly among the different methods employed (Fig. 2). Habitat loss estimated from reduction in the area of occupancy (AOO) was also significantly lower than the estimated forest cover loss (~50%) for Sabah as a whole (Mean = 41%, Single sample *t*-test: $t = -2.36$, df = 32, $P = 0.025$). This difference may reflect a collecting bias as a majority of herbarium specimens were obtained from protected areas or in production forest reserves under natural forest management. As the estimate of habitat loss based on the reduction in AOO is determined from the number of sites that retain the species, a bias towards collecting within protected areas will under-estimate habitat loss within the wider unprotected landscape. At least 30 percent of all dipterocarp voucher specimens recorded on the database maintained by the Forest Research Centre (Sabah Forestry Department, unpublished data) were collected from the protected areas of Sabah, which represent just 11 percent of the total land surface area of the state. Collection effort is also strikingly biased among protected areas: for example, approximately 7 percent of the specimens (380 collections from 63 species) were collected within the 4294 ha Kabili-Sepilok Forest Reserve, while only 0.2 percent of the specimens (12 specimens from 7 species) were collected in the ten-fold larger Danum Valley Conservation Area. This collecting bias is likely to be replicated across all plant taxa and invalidates the use of reduction in AOO to determine their conservation status.

Mean habitat loss estimates based on reduction in the extent of occurrence (EOO) and ecological niche models were significantly higher than the estimated forest cover loss for Sabah as a whole (means of 58 and 63%, respectively; single sample t-test: $t = 4.66$, df = 32, $P = 0.00006$ and $t = 4.36$, df = 32, $P = 0.0001$, respectively). The estimates of habitat loss determined as a function of reduction in extent of occurrence (EOO) varied less among species (Fig. 1b) than estimates obtained from either ecological niche modelling (Fig. 1a) or from reduction in AOO (Fig. 1c).

Estimates of habitat loss based on reduction in EOO did not differ between lowland, ultramafic and upland/montane species. This outcome was unexpected because the extent of forest loss has been much greater for lowland forest types (55.3 to 82.4% of original forest cover) than for ultramafic (8.5 to 31.4% of original area) or upland/montane (26.5 to 46.0% of original area) forest types (Table S1). The EOO polygons for the ultramafic and upland/montane species include areas of lowland habitat that have experienced greater rates of forest loss than neighbouring ultramafic and upland/montane areas, which leads to an overestimation of habitat loss for species that are only found within the ultramafic or upland/montane environments.

Conversely the EOO polygons for the lowland species often contain patches of ultramafic and upland/montane forest, leading to an underestimation of habitat loss for these species. This approach also had low ability to identify the species that are most in need of conservation action, as all species were classified with approximately the same threat category (Figure 1b). This problem might be ameliorated by alternative algorithms for calculating the EOO, such as the α-hull approach (IUCN Standards and Petitions Subcommittee 2010). However, the α-hull approach was not suitable for our assessments because of the low number of collection localities for many species and the uncertain effects of the inherent collection bias in the data-set.

Ecological niche modelling has the potential to be a powerful tool to support conservation decision making in the tropics, but pervasive problems with data quality and availability need to be overcome before this potential can be fully realized (Cayuela *et al.* 2009). Notwithstanding these limitations, our niche models can be used to suggest tentative conservation priority setting for a range of dipterocarp species and to target specific localities (Fig. 1a). For example, lowland species confined to the north coast of Sabah, such as *Dipterocarpus lamellatus* and *Shorea kudatensis,* have suffered a higher proportional habitat loss, and should have a higher priority for conservation, than species that occur on the east coast. However, ENM techniques should be used cautiously for identifying conservation priorities. Niche models will over-predict a species' distribution if barriers to dispersal or biotic interactions exclude the species from a particular part of its potential niche (Phillips *et al.* 2006). Conversely, ENMs will under-predict species distributions for dipterocarps if a species occurs naturally on soil associations that are not represented in the sample. For example, if all collection localities of any one soil association are removed separately from the data-set for *Dipterocarpus grandiflorus* the range size predicted by the distribution model is reduced to 45 – 98 percent of that predicted by the entire data-set. To evaluate the extent of over- or under-prediction of dipterocarp species distributions we are currently field-testing the model predictions reported in this paper, and expanding our database to ensure that all soil associations have been sampled (Maycock et al. unpublished data).

LIMITATIONS TO ESTIMATES OF HABITAT LOSS —Conservation assessments should attempt to assess each species using as many of the IUCN criteria as possible, but this target is impossible for most tropical plants. Many assessments are based primarily on Criterion B, which is the extent of a species geographic range. The IUCN Standards and Petition Subcommittee (2010) points out that Criterion B is frequently misused, and may not be suitable for application at a regional scale (Miller *et al.* 2005). In this study we focused on the IUCN's criterion A, which relies on estimation of the decline in the population size, either through direct observation or by reduction in the AOO, EOO and/or habitat quality. Criterion A was selected because assessing the proportion of remaining habitat within a species' range is more appropriate for a regional assessment than measuring the size of its geographic range (McIntyre 1992). The protocol for assessments made using Criterion A states that all habitat loss must have occurred within three generations for the target species. Documentation of forest loss in Sabah only goes back to 1957, at which time forest cover had been reduced to 86 percent of its original extent (McMorrow & Talip, 2001). It is likely, however, that natural forests would have covered the entire state prior to the initiation of forest exploitation in the 1890s (McMorrow & Talip, 2001), which is within a single generation time from the present day for long-lived trees such as dipterocarps.

Our approach assumes that all land not gazetted as a production forest or protected area has no populations of the species examined. Contrary to this assumption, during surveys to ground-truth the niche models, we have discovered small (1 –20 individuals) remnant populations of *Dipterocarpus ochraceus* and *Shorea kudatensis* outside forest reserves and protected areas. These populations have no legal protection, however, and continue to be exploited. Many sites also showed signs of fire damage and had high populations of invasive alien species (the tree *Acacia mangium* and the grass *Imperata cylindrica*), and no evidence of dipterocarp regeneration (C.R. Maycock *et al.*, unpubl. data). In 2001, less than 7 percent of Sabah's natural forests were found outside the permanent forest estate or protected areas, and this proportion is likely to have continued to decline since then (Sabah Forestry Department, unpubl. data). Further field surveys are required to ascertain the extent and conservation value of the forested areas outside forest reserves and protected areas, especially for species, such as *Shorea kudatensis*, that are predicted to be present in these areas based on the species distribution models.

Our approach also assumes that all the protected areas and production forests managed under natural forest management retain natural forest. In reality, approximately 10 percent of the ~540,000 ha of protected areas that were surveyed during the Conservation Areas Information and Monitoring System (Sabah Forestry Department 2005) were heavily degraded and supported little natural vegetation. A much larger proportion of the production forest is likely to be heavily degraded. The incorporation of forest condition maps into the GIS may allow us to classify the quality of the remaining habitat (Imai *et al.* 2009, Sabah Forestry Department 2009), but this will only be possible when adequate data are available for all forest reserves and protected areas.

Variations in dipterocarp population density among species introduce uncertainty into estimates of population size, which are required for conservation assessments. Natural densities of potentially reproductive dipterocarps vary by three orders of magnitude across species, from tens of individuals per ha for the common species down to 1 to 10 individuals per 1000 ha for the very rare species (Lee *et al.* 2002). Population densities also vary across the landscape according to soil and topographic associations (Lee *et al.* 2002). For most species considered in this paper, harvesting would have reduced the density of large trees in production forests under natural forest management, and in some protected areas, as they are of commercial importance and have been over-exploited in the past (Mannan & Awang 1997). Such factors are likely to be especially critical where species differ in their vulnerability to the effects of fragmentation (Kettle *et al*. 2011a, Kettle *et al.* 2011b).

CONSERVATION ASSESSMENTS.— Conservation assessments based on habitat loss estimated from the ecological niche models suggest that the Sabah populations of four species (12%) should be classified as critically endangered, 23 (70%) as endangered, five (15%) as vulnerable and one (3%) as of least concern (Table S2). We found only limited agreement between our assessments and those reported by previous authors (Table 1). The global assessments (IUCN 2010) recorded a higher category of threat for most species than estimated by our study. The difference between our assessments and the global assessments may reflect a genuine difference in the degree of endangerment of the species at regional and global scales, or differences in methods. The proportion of forest lost within Southeast Asia varies from ~30 to 97 percent between different territories (FAO 2006), which could lead to differences between regional and global conservation assessments for individual species. Sixty one percent of the dipterocarps of Sabah that have been assessed are currently listed as critically endangered (IUCN 2010). These global assessments were based largely on the perceptions of an expert assessor, as little or no quantitative data were available to support the assessments. Some of these global assessments have been contradicted by the subsequent regional assessments of the assessor (Ashton 2004), and the global assessments of all the species examined in this study are acknowledged by IUCN (2010) as in need of upgrading.

We found only limited agreement between our assessments and those in the Malaysia Plant Red List (Chua *et al.* 2010). Of the 11 species examined in both studies, the Sabah populations of only three were considered by Chua *et al.* (2010) to be threatened and these were classified at the lowest level of threat (vulnerable). As Sabah has lost at least 35 percent of its forest cover in the last 60 years, it is likely that the assessments of Chua *et al.* (2010) underestimate the degree of threat. This difference in threat assessments may be associated with the different criteria used to make the assessments. Chua *et al.* (2010) determined the extent of occurrence for each species and classified each species primarily on the extent of their geographical range (Criterion B). This measure does not take into account habitat loss and only prioritizes species with narrow geographical ranges, which may under-estimate the number of species at risk from widespread habitat loss (McIntyre 1992). Our assessments corresponded more closely to those of Ashton (2004), but with some notable exceptions (Table 2). For example, Ashton (2004) listed *Shorea micans* as critically endangered, while our assessments of this species classified it as of least concern (AOO and ENM) or endangered (EOO). As this species is found primarily in ultramafic forests, which have experienced some of the lowest amounts of habitat loss (8.5 to 31.4%, Table S1), it is unlikely that the Sabah population of this species is endangered based on estimates of habitat loss alone, although other factors such as degradation by fire may affect its conservation status. Additionally, Ashton's (2004) assessments addressed the status of the species' populations in both Sabah and Sarawak, and there may be differences in their conservation status between the two states.

FUTURE PROSPECTS FOR DIPTEROCARP CONSERVATION IN SABAH.—The Aichi 2020 targets call for the prevention of extinction of threatened species (Secretariat of the Convention on Biological Diversity 2010). Achieving this target will require a better understanding of which species are threatened at both regional and international scales. Some of the damaging effects of unsustainable forest management are being addressed by restoration of degraded areas with indigenous tree species (Mannan & Awang 1998, Sabah Forestry Department 2008), and the protection of High Conservation Value Forest as part of the state-wide implementation of reduced impact logging within the production forest reserves. Nonetheless, few of these schemes are linked to conservation of critically endangered plant species and are primarily focused on the presence of charismatic mega fauna. If future extinctions of threatened tree and other plant species are to be prevented, and the Aichi 2020 Biodiversity targets met, accurate estimates of the distribution and conservation status of the remaining species are required. If this objective cannot be achieved for well-known and commercially important taxa such as dipterocarps, then there is little hope that any progress will be made on assessing the thousands of other lesser-known plant species in Sabah. Our study presents a cost effective alternative strategy for conservation assessments that should be integrated into projects targeting conservation and restoration of dipterocarp forests (Kettle *et al* 2011a).

Responsibility for plant conservation in Sabah lies with the State Government, and administration of forest reserves and protected areas is devolved to the Sabah Forestry

Department and the Sabah State Parks respectively. Resources for conducting assessments of plant conservation status are limited, and plant biodiversity is high (Ashton 2008). Therefore there is a need for a cost effective and rapid assessment technique that will be of use to land-use planners. In order to allow land–use planners to examine how future land-use decisions will affect biodiversity, the information provided by the assessment technique needs to be spatially explicit and must identify priority sites for conservation that harbour multiple threatened species (Callmander *et al.* 2005). Combined with additional ground-truthing and model validation, we aim to apply the ecological niche modelling approach outlined in this paper as the basis of such a system.

ACKNOWLEDGMENTS

The authors would like to thank the numerous Forestry Research Centre staff who have contributed to the recent surveys. This work draws heavily on data collected as part of the Heart of Borneo and Conservation Area Information and Management System projects and we appreciate the effort of the field staff of those projects. The project would not have been possible without the dedicated plant collecting efforts of the numerous past and present forest botanists, ecologists, foresters, tree climbers and research assistants of the Sabah Forestry Department. We thank the Director of Forestry Datuk Sam Mannan for support. This work was supported by the Sabah State Government by a grant award to EK under the 9th and 10th Malaysia Plans, a grant from the UK Natural Environment Research Council to DB and a training award from the Universiti Kelantan Malaysia to ANA.

LITERATURE CITED

ABELI, T., R. GENTILI, G. ROSSI, G. BEDINI, AND B. FOGGI. 2009. Can the IUCN criteria be effectively applied to peripheral isolated plant populations? Biodiversity Conserv. 18: 3877-3890.

ASHTON, P. S. 2004. Dipterocarpaceae. *In* E. Soepadmo, L. G. Saw and R. C. K. Chung (Eds.) Tree flora of Sabah & Sarawak, Volume 5, pp 63-388. Forest Research Institute Malaysia, Kuala Lumpur, Sabah Forestry Department, Sandakan & Sarawak Forestry Department, Kuching, Malaysia.

ASHTON, P. S. 2008. Changing values of Malaysian forests: the challenge of biodiversity and its sustainable management. J. Trop. For. Sci. 20: 282-291.

ASHTON, P.S. 2010. Conservation of Borneo biodiversity: do small lowland parks have a role, or are big island sanctuaries sufficient? Brunei as an example. Biodiversity Conserv. 19: 343–356.

ASIA PACIFIC FORESTRY COMMISSION. 2010. Forests and biodiversity: Conservation and sustainable use of forest treasures. Available at http://www.fao.org/docrep/meeting/018/ak839e.pdf (accessed 23 November 2010).

BRUMMITT, N., S. P. BACHMAN, AND J. MOAT. 2008. Applications of the IUCN Red List: towards a global barometer for plant diversity. Endang. Species Res. 6: 127-135.

CALLMANDER, M. W., G. E. SCHATZ, AND P. P. LOWRY II. 2005. IUCN Red List assessment and the Global Strategy for Plant Conservation: taxonomists must act now. Taxon 54: 1047-1050.

CALLMANDER, M. W., G. E. SCHATZ, P. P. LOWRY II., M. O. LAIVAO. J. RAHARIMAMPIONONA, S. ANDRIAMBOLOLONERA, T. RAMINOSOA, AND T. CONSIGLIO 2007. Application of IUCN Red List criteria and assessment of Priority Areas for Plant Conservation in Madagascar: rare and threatened Pandanaceae indicate new sites in need of protection. Oryx 41: 168-176.

CANNON, C. H., AND M. LEIGHTON. 2004. Tree species distributions across five habitats in a Bornean rain forest. J. Veg. Sci. 15: 257-266.

CAYUELA, L., D. J. GOLICHER, A. C. NEWTON, M. KOLB, F. S. DE ALBURQUERQUE, E. J. M. M. ARETS, J. R. M. ALKEMADE, AND A. M. PÉREZ. 2009. Species distribution modeling in the tropics: problems, potentialities, and the role of biological data for effective species conservation Tropical Conservation Science 2: 319-352. Available at www.tropicalconservationscience.org (accessed November 15, 2010).

CHEN, H. K. 2004. A Malaysian assessment of The World List of Threatened Trees. Available at www.traffic.org/forestry-reports/traffic_pub_forestry1.pdf (accessed November 28, 2010).

CHUA, L. S. L., M. SUHAIDA, M HAMIDAH, AND L. G. SAW. 2010. Malaysia Plant Red List: Peninsular Malaysian Dipterocarpaceae. Forest Research Institute Malaysia Research Pamphlet 129.

DAVIS, S. J., S. TAN, J. V. LAFRANKIE, AND M. D. POTTS. 2005. Soil-related floristic variations in a hyper-diverse dipterocarp forest. *In* D. W. Roubik, S. Sakai and A. A. Hamid (Eds.). Pollination Ecology of the Rain Forest: Sarawak Studies. Springer, New York.

ELITH, J., C. H. GRAHAM, R. P. ANDERSON, M. DUDÍK, S. FERRIER, A. GUISAN, R. J. HIJMANS, F. HUETTMANN, J. R. LEATHWICK, A. LEHMANN, J. LI, L. G. LOHMANN, B. A. LOISELLE, G. MANION, C. MORITZ, M. NAKAMURA, Y. NAKAZAWA, J. MCC. OVERTON, A. T. PETERSON, S. J. PHILLIPS, K. RICHARDSON, R. SCACHETTI-PEREIRA, R. E. SCHAPIRE, J. SOBERÓN, S. WILLIAMS, M. S. WISZ, AND N. E. ZIMMERMANN. 2006. Novel methods improve prediction of species' distributions from occurrence data. Ecography 29: 129-151.

FITZPATRICK, Ú., T. E. MURRAY, R. J. PAXTON, AND M. J. F. BROWN. 2007. Building on IUCN regional red lists to produce list of species of conservation priority: a model with Irish bees. Conserv. Biol. 21: 1324-1332.

FAO. 2006. Global forest resources assessment 2005: progress towards sustainable forest management. Forestry paper 147. FAO (United Nations Food and Agriculture Organization), Rome.

GASTON, K. J, AND R. A. FULLER. 2009. The sizes of species' geographic ranges. J. Appl. Ecol. 46: 1-9.

GRAHAMS, C. H., J. ELITH, R. J. HIJMANS, A. GUISAN, A. T. PETERSON, B. A. LOISELLE, AND THE NCEAS PREDICTING SPECIES DISTRIBUTIONS WORKING GROUP. 2008. The influence of spatial errors in species occurrence data used in distribution models. J. Appl. Ecol. 45: 239-247.

HIJMANS, R.J., K. A. GARRETT, Z. HUAMAN, D. P. ZHANG, M. SCHREUDER, AND M. BONIERBALE. 2000. Assessing the geographical representativeness of genebank collections: the Bolivian wild potatoes. Conserv. Biol. 14: 1755-1765.

HIJMANS, R.J., L. GUARINO, A. JARVIS, R. O'BRIEN, P. MATHUR, C. BUSSINK, M. CRUZ, I. BARRANTES, AND E. ROJAS. 2005. *DIVA-GIS Version 5.2 manual.* Available at: www.diva-gis.org (accessed 2 June 2009).

IMAI, N., H. SAMEJIMA, A. LANGNER, R. C. ONG, S. KITA, J. TITIN, A. Y. C. CHUNG, P. LAGAN, Y. F. LEE, AND K. KITAYAMA. 2009. Co-benefits of sustainable forest management in biodiversity conservation and carbon sequestration. PLOS One 4: E8267. DOI:10.1371/JOURNAL.PONE.0008267

IRFAN-ULLAH, M., G. AMARNATH, M. S. R. MURTHY, AND A. T. PETERSON. 2007. Mapping the geographic distribution of *Aglaia bourdillonii* Gamble (Meliaceae), an endemic and threatened plant, using ecological niche modeling. Biodiversity Conserv. 16:1917–1925.

IUCN. 2010. IUCN Red List of Threatened Species. Version 2010.3. Available at http://www.iucnredlist.org (accessed November 2, 2010).

IUCN STANDARDS AND PETITIONS SUBCOMMITTEE. 2010. Guidelines for using the IUCN Red List categories and criteria. Version 8.1. Prepared by the Standards and Petitions Subcommittee in March 2010. Available at http://intranet.iucn.org/webfiles/doc/SSC/RedList/RedListGuidelines.pdf (accessed August 10, 2010).

KETTLE, C.J., J. GHAZOUL, P.S. ASHTON, C.H. CANNON, L. CHONG, B. DIWAY, E. FARIDAH, R. HARRISON, A. HECTOR, P. HOLLINGSWORTH, L.P. KOH, E. KHOO, K, KITAYAMA, K. KARTAWINATA, A.J. MARSHALL, C.R. MAYCOCK, S. NANAMI, G. PAOLI, M.D. POTTS, I. SAMSOEDIN, D. SHEIL, S. TAN, I. TOMOAKI, C. WEBB, T. YAMAKURA, AND D.F.R.P. BURSLEM, 2011a. Seeing the fruit for the trees in Borneo. Conserv. Letters, NO. DOI: 10.1111/j.1755-263X.2010.00161.x.

KETTLE, C.J., C.R. MAYCOCK, J. GHAZOUL, P.M. HOLLINGSWORTH, E. KHOO, R.S.H. SUKRI, AND D.F.R.P. BURSLEM. 2011b. Ecological Implications of a Flower Size/Number Trade-Off in Tropical Forest Trees. PLoS ONE 6, e16111.

LEE, H. S., S. J. DAVIES, J. V. LAFRANKIE, S. TAN, T. YAMAKURA, A. ITOH, T. OHKUBO, AND P. S. ASHTON. 2002. Floristic and structural diversity of mixed dipterocarp forest in Lambir Hills National Park, Sarawak, Malaysia. J. Trop. For. Sci. 14: 379-400.

MANNAN, S., AND Y. AWANG. 1997. Sustainable forest management in Sabah. Proceedings Seminar on Sustainable Forest Management, Vol 27, pp 51-74. Sabah Forestry Department, Sandakan.

MCINTYRE, S. 1992. Risks associated with the setting of conservation priorities from rare plant species lists. Biol. Conserv. 60: 31-37.

MCMORROW, J., AND M. A. TALIP. 2001. Decline of forest area in Sabah, Malaysia: Relationship to state policies, land code and land capability. Global Environ. Change 11: 217-230.

MILLER, R., J. P. RODRÍGUEZ, C. BAMBARADENIYA, R. BOLES, M. EATON, T. FOWLER, U. GÄRDENFORS, V. KELLER, S. MOLUR, C. POLLOCK, AND S. WALKER. 2005. Analysis of the application of IUCN Red List criteria at a national level. NRLAG Workshop Report.

MINISTRY OF SCIENCE, TECHNOLOGY AND THE ENVIRONMENT. 1998. National Policy in Biological Diversity. Available at http://www.arbec.com.my (accessed 28 November 2010).

MOAT, J. 2007. Conservation assessment tools. Extension for ArcView 3.x, version 1.2. GIS Unit, Royal Botanic Gardens, Kew. Available at http://www.rbgkew.org.uk/gis/cats (accessed 1 June 2010).

NAEEM, S., D.E. BUNKER, A. HECTOR, M. LOREAU, AND C. PERRINGS. 2008. Eds. Biodiversity, Ecosystem Functioning, and Human Wellbeing. Oxford University Press, Oxford.

NIC LUGHADHA, E., J. BAILLIE, W. BARTHLOTT, N. A. BRUMMITT, M. R. CHEEK, A. FARJON, R. GOVAERTS, K. A. HARDWICK, C. HILTON-TAYLOR, T. R. MEAGHER, J. MOAT, J. MUTKE, A. J. PATON, L. J. PLEASANTS, V. SAVOLAINEN, G. E. SCHATZ, P. SMITH, I. TURNER, P. WYSE-JACKSON, AND P. R. CRANE. 2005. Measuring the fate of plant diversity: towards a foundation for future monitoring and opportunities for urgent action. Phil. Trans. R. Soc. Lond. B 360: 359-372.

PAOLI, G. D., L. M. CURRAN, AND D. R. ZAK. 2006. Soil nutrients and beta diversity in the Bornean Dipterocarpaceae: evidence for niche partitioning by tropical rain forest trees. J. Ecol. 94: 157–170.

PHILLIPS, S. J., R. P. ANDERSON, AND R. E. SCHAPIRE. 2006. Maximum entropy modeling of species geographic distributions. Ecol. Model. 190: 231-259.

PHILLIPS, S. J., AND M. DUDÍK. 2008. Modeling of species distribution with Maxent: new extensions and a comprehensive evaluation. Ecography 31: 161-175.

R DEVELOPMENT CORE TEAM. 2010. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL Avaiable at http://www.R-project.org (accessed 10 November 2010).

SABAH FORESTRY DEPARTMENT. 2005. Conservation Areas Information and Monitoring System. Available at http://www.forest.sabah.gov.my/caims (accessed 22 November 2010).

SABAH FORESTRY DEPARTMENT. 2008. Annual Report 2008. Sabah Forestry Department, Sandakan, Malaysia.

SABAH FORESTRY DEPARTMENT. 2009. High conservation value forest (HCVF) in FMU 17. SFM Division, Sabah Forestry Department, Sandakan, Malaysia.

SCHERBER, C., N. EISENHAUER, et al. 2010. Bottom-up effects of plant diversity on multitrophic interactions in a biodiversity experiment. Nature 468: 553-556.

SECRETARIAT OF THE CONVENTION ON BIOLOGICAL DIVERSITY. 2002. Global Strategy for Plant Conservation. Secretariat of the Convention on Biological Diversity, Montreal, Quebec, Canada.

SECRETARIAT OF THE CONVENTION ON BIOLOGICAL DIVERSITY. 2010. Proposals for a consolidated update of the Global Strategy for Plant Conservation 2011-2020. Secretariat of the Convention on Biological Diversity.

SODHI, N. S., M. R. C. POSA, T. M. LEE, D. BICKFORD, L. P. KOH, AND B. W. BROOK. 2010. The state and conservation of Southeast Asian Biodiversity. Biodiversity Conserv. 19: 317–328.

SOLANO, E., AND T. P. FERIA. 2007. Ecological niche modeling and geographic distribution of the genus *Polianthes* L. (Agavaceae) in Mexico: using niche modeling to improve assessments of risk status. Biodiversity Conserv. 16:1885–1900.

SUKRI, R.S., R.A. WAHAB, K.A. SALIM, AND D.F.R.P. BURSLEM. IN PRESS. Habitat associations and community structure of dipterocarps in response to environment and soil conditions in Brunei Darussalam, Northwest Borneo. Biotropica.

WISZ, M. S., R. J. HIJMANS, J. LI, A. T. PETERSON, C. H. GRAHAM, A. GUISAN, AND NCEAS PREDICTING SPECIES DISTRIBUTIONS WORKING GROUP. 2008. Effects of sample size on the performance of species distribution models. Diversity Distrib.14: 763–773.

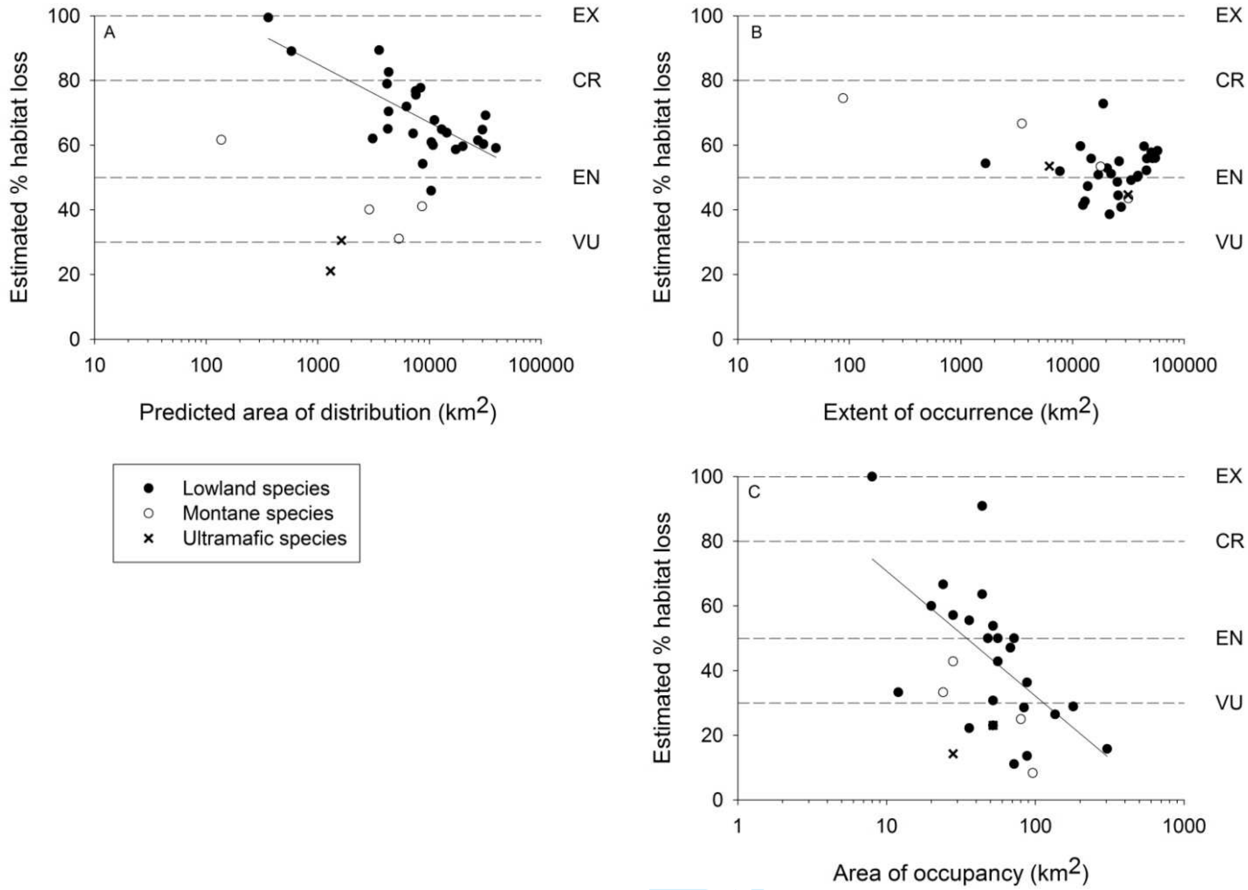
Table 1. A comparison of threat categories from the IUCN Red List (IUCN 2010), Ashton (2004), Chua *et al.* (2010) and this study for 33 dipterocarp species in Sabah. The IUCN red list is the global assessment of the study species, Ashton (2004) is an assessment over Sabah and Sarawak, while Chua *et al.* (2010) and this study cover the assessment for these species in Sabah only. The *P* values for the pair-samples Wilcoxon test are presented below for comparisons of the distribution of species among threat categories.

Threat category	Source			This study		
	IUCN Red list	Ashton 2004	Malaysian Red list	ENM	EOO	AOO
Extinct	0	1	0	0	0	1
Critically endangered	20	5	0	4	1	1
Endangered	2	12	0	23	25	11
Vulnerable	0	13	3	5	6	8
Near threatened	0	0	7	0	0	0
Least concerned	0	2	1	1	0	12
Not evaluated	11	0	23	0	0	0
Date deficient	-	-	-	0	1	0
Wilcoxon test	Source			This study		

	IUCN Red list	Ashton 2004	Malaysian Red list	ENM	EOO	AOO
IUCN Red List		0.001	0.003	< 0.001	< 0.001	< 0.001
Ashton 2004			0.001	0.116	0.676	0.001
Malaysian Red List				0.001	0.002	0.029
ENM					0.179	< 0.001
EOO						0.002

FIGURE 1 Relationships between habitat loss and (A) predicted area within the historic distribution, (B) extent of occurrence and (C) area of occupancy for 33 dipterocarp species in Sabah. The IUCN threat categories under criteria A2 are listed at the side of the figure. These categories correspond to the percentage decline in habitat with Vulnerable (VU), Endangered (EN), Critically Endangered (CR) and Extinct (EX) corresponding to a 30, 50, 80 and 100% decline in habitat respectively. The solid lines indicate the significant relationship between habitat loss and predicted area of distribution or area of occupancy for the 27 lowland species.

FIGURE 2 Comparison of estimates of percentage habitat loss determined by the ecological niche modelling technique compared to (A) reduction in the extent of occurrence (EOO) and (B) area of occupancy (AOO), and (C) a comparison of the two IUCN methods. The boxes indicate the thresholds for IUCN threat categories under criteria A2; points outside these boxes indicate where the two assessment methods estimate different categories of threat. The dotted line (slope = 1) is used to indicate differences in the estimates of percent habitat loss and codes correspond to IUCN threat categories (LC, least concern; VU, vulnerable; EN, endangered; CR, critically endangered).


A
B
C
Estimated % habitat loss
Predicted area of distribution (km2)
Extent of occurrence (km2)
Area of occupancy (km2)
EX
CR
EN
VU
Lowland species
Montane species
Ultramafic species

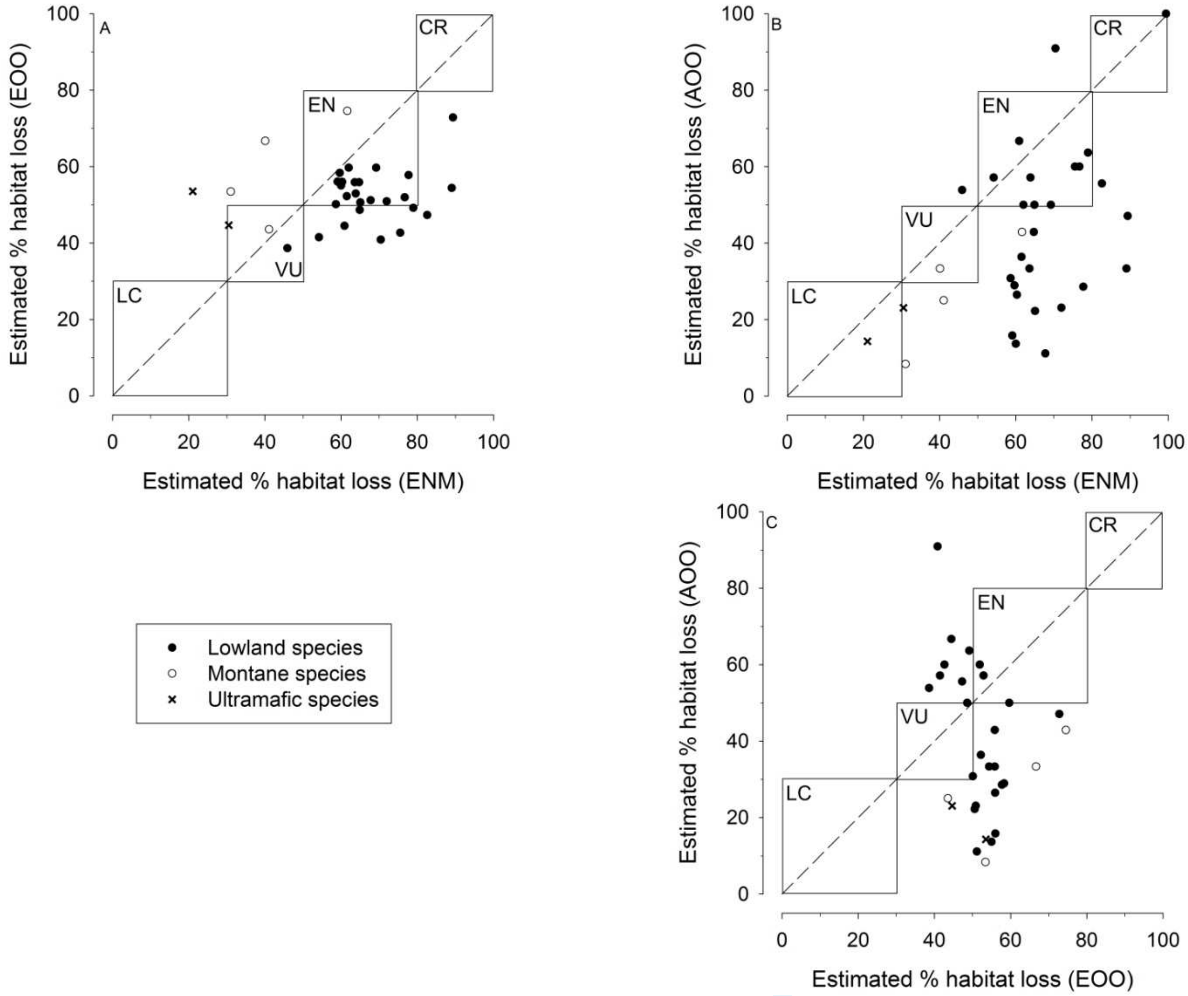

A
B
C
LC
VU
EN
CR
Estimated % habitat loss (EOO)
Estimated % habitat loss (AOO)
Estimated % habitat loss (ENM)
0
20
40
60
80
100
Lowland species
Montane species
Ultramafic species

Table S1. Estimated percent habitat loss across the twelve major forest types found in Sabah. Estimates of percentage habitat loss among the different forest types was determined by overlaying the current land-use map over a natural forest cover map of Sabah (Sabah Forestry Department, unpubl. data) in DIVA GIS and determine the percentage of area outside of the permanent forest estate or protected areas.

Forest type	Estimate % area of Sabah	Estimate % of original area converted to alternative land use
Beach forest	0.7	70.4
Lowland mixed dipterocarp	47.2	67.8
Lowland mixed dipterocarp and kerangas	6.9	69.1
Lowland peatswamp	1.6	55.3
Lowland freshwater swamp	1.0	74.7
Lowland seasonal freshwater swamp	3.5	82.4
Lowland ultramafic	1.3	31.4
Upland mixed dipterocarp	18.5	46.0
Upland mixed dipterocarp and kerangas	5.7	18.3
Upland ultramafic	1.1	8.5
Lower montane kerangas	3.6	31.7

Lower montane forest	2.6	26.5

Table S2. The provisional regional threat category determined by this study and the IUCN global threat category from IUCN (2010) for 33 dipterocarp species, where EN is endangered, CR is critically endangered (CR) and NE is not evaluated. The capital letters following the IUCN global threat category refer to the assessment criteria, where A is the population reduction, B the size of the geographic range, C used for species with small population in decline and D for very small or restricted populations. Threshold values for each of these criteria can be found in the IUCN Guidelines for using the IUCN Red list Categories and Criteria (IUCN Standards and Petitions Subcommittee 2010). The area under the curve (AUC) of the receiver operating characteristic for the test runs of the ecological niche models are given.

Habitat and species	Regional threat category	IUCN global threat category	AUC
Lowland			
Dipterocarpus acutangulus	EN	NE	0.881
Dipterocarpus applanatus	EN	CR A1cd, B1+2c	0.826
Dipterocarpus caudiferus	EN	NE	0.795
Dipterocarpus confertus	EN	NE	0.798
Dipterocarpus conformis	EN	NE	-
Dipterocarpus costulatus	EN	CR A1cd+2cd, B1+2c	-

Dipterocarpus crinitus	CR	EN A1cd+2cd	-
Dipterocarpus fusiformis	EN	CR A1cd+2cd, B1+2c	-
Dipterocarpus geniculatus ssp *grandis*	EN	NE	0.912
Dipterocarpus gracilis	EN	CR A1cd+2cd	0.823
Dipterocarpus grandiflorus	EN	CR A1cd+2cd	0.948
Dipterocarpus hasseltii	EN	CR A1cd+2cd	-
Dipterocarpus humeratus	EN	NE	0.860
Dipterocarpus kerrii	EN	CR A1cd+2cd, B1+2c	0.821
Dipterocarpus kunstleri	EN	CR A1cd+2cd	0.736
Dipterocarpus lamellatus	CR	CR A1cd+2cd, B1+2c, C1, D	-
Dipterocarpus stellatus ssp *parvus*	EN	NE	0.849
Dipterocarpus tempehes	EN	CR A1cd+2cd, B1+2c	0.890
Dipterocarpus verrucosus	EN	NE	0.894
Hopea aequalis	CR	CR A1c, B1+2c, C1	-
Hopea mengerawan	EN	CR A1cd, B1+2c	-
Hopea plagata	EN	CR A1cd, B1+2c	-

Hopea wyatt-smithii	EN	CR A1c+2c, B1+2c	0.904
Shorea almon	EN	CR A1cd	0.890
Shorea kudatensis	CR	CR A1cd, C2a	
Shorea ochracea	VU	NE	0.934
Shorea waltonii	EN	CR A1cd	
Upland/montane			
Dipterocarpus ochraceus	EN	NE	-
Hopea montana	VU	CR B1+2c, D	-
Shorea monticola	VU	NE	0.955
Shorea platyclados	VU	EN A1cd	0.920
Ultramafic			
Dipterocarpus lowii	VU	CR A1cd+2cd, B1+2c	0.844
Shorea micans	LC	CR A1c, C2a	0.956