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Protected areas of Borneo fail to protect forest landscapes with high habitat connectivity

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Abstract Throughout the world, previously extensive areas of natural habitats have been degraded and fragmented, and improving habitat connectivity may help the long-term persistence of species, and their ability to adapt to climate changes. We focused on Borneo, where many remaining areas of tropical forest are highly fragmented, and we assessed the extent to which Protected Areas (PAs) protect highly-connected forest sites. We analysed remotely-sensed land cover data (0.86 km^2 grid cell resolution) using 'Zonation' reserve design software, and we ranked grid cells (rank 0–1) according to forest extent and connectivity. PAs currently cover 9% of Borneo, but <20% of highly-connected cells (i.e. cells with Zonation ranks $\geq$0.9) lie within PAs. Approximately 65% of highly-connected cells were located above 400 m elevation, although >60% of Borneo's total land area lies below 200 m and only 15% of highly-connected cells occurred in these low elevation areas. These findings were relatively insensitive to assumptions about species' dispersal ability (within the range 1–20 km; representing relatively mobile animal species). The percentage of highly-connected grid cells within PAs could rise from <20 to >50% under proposed new PAs (including the 'Heart of Borneo' project), although many other highly-connected sites will remain unprotected. On-going land-use changes mean that existing PAs in lowland areas are likely to become increasingly isolated within inhospitable agricultural landscapes, and improving connectivity through reforestation and rehabilitation of degraded forest may be required to maintain the conservation value of these PAs in future.

Keywords Landscape permeability · Reserve design · SE Asia · Landscape prioritization · Climate change adaptation

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Introduction

Tropical rainforests are one of the most diverse ecosystems on Earth, but land-use changes have resulted in widespread forest degradation and deforestation (Wright 2005; Gibbs et al. 2010; Hansen et al. 2010). Many areas of tropical forest are highly fragmented, leading to changes in ecological processes and population dynamics within forest fragments (Terborgh et al. 2001; Morris 2010), and presenting a serious threat to biological diversity (The Convention on Biological Diversity (www.cbd.int); Brook et al. 2003; Sodhi et al. 2010). Populations of species within habitat patches can become isolated, resulting in increased likelihood of inbreeding and genetic erosion in the long-term (Lande 1988; Brook et al. 2002; Benedick et al. 2007b). In temperate regions, reduced genetic diversity is associated with increased incidence of local extinction (Saccheri et al. 1998), thus conserving networks of well-connected habitats is important for promoting species persistence in fragmented landscapes (Hanski 1999). The spatial distribution and extent of habitat is also important for helping species respond to climate changes by facilitating dispersal and helping species shift their distributions and colonise newly-available habitats (Beier and Noss 1998; Hill et al. 2001; Vos et al. 2008; Heller and Zavaleta 2009; Hodgson et al. 2009, 2011, in press; Carroll et al. 2010). However, the degree to which current Protected Areas (PAs) conserve highly-connected habitats and thus may contribute to adaptation of species to climate change and promote species' ability to persist in fragmented landscapes has received little attention (Hannah 2010).

The Island of Borneo in SE Asia has extensive areas of tropical rainforest. Lowland forests of Borneo are dominated by trees of the family *Dipterocarpaceae*, which are important timber trees, and many areas are reserved as production forests which are selectively logged (Sodhi et al. 2010). Many other areas of forest have been converted to other land uses, particularly oil palm (*Elaeis guineensis*) plantations, and forest areas of Borneo have been reduced by more than half since the 1940s (McMorrow and Talip 2001). Although pristine forest has the greatest conservation value, the conservation value of production forest can be high (Berry et al. 2010; Edwards et al. 2011), but conversion of forest to oil palm plantations considerably reduces species diversity (Fitzherbert et al. 2008; Koh and Wilcove 2008), and thus PAs are important for conserving forest species in these agricultural landscapes. However, these PAs may become increasingly isolated in future if land-use changes continue, and the conservation of biological diversity in this region will depend on avoiding further forest degradation and encroachment (Curran et al. 2004), and increasing the extent of forest that is protected. In recognition of the importance of conserving forest areas, WWF aims to protect a network of PAs on Borneo within the proposed trans-boundary 'Heart of Borneo' protected area project (WWF 2005), and we examine whether this project will increase the conservation of highly-connected forest areas.

The Millennium Ecosystem Assessment (2005) identified five main environmental drivers of biodiversity loss, including climate and habitat changes, and all drivers are predicted to have increased detrimental impacts on biological diversity in tropical forests in future. There is evidence that species from temperate (e.g. Warren et al. 2001; Hickling et al. 2006), and tropical regions (Colwell et al. 2008; Chen et al. 2009, 2011) are shifting their distributions in response to climate change, but loss of habitat is slowing down and/or halting species' range shifts (Hill et al. 2001). Thus, the distribution, quality and extent of habitat is likely to be important for conserving many species in future (Hodgson et al. 2009), and improving habitat connectivity is an aim of many conservation management plans. In tropical regions, locations with high species richness and/or endemicity are usually selected for protection (Myers et al. 2000), and here we argue that the connectivity of locations should also be considered (Hannah 2010).

In this study we use ‘Zonation’ reserve design software (Moilanen and Kujala 2008) to prioritise the conservation value of forest areas on Borneo, based on forest extent and connectivity with other areas of forest. Zonation has been used in a variety of contexts, for example in identifying important areas for conserving species (Kremen et al. 2008; Franco et al. 2009; Carroll et al. 2010), and for selecting new areas for protection (Lehtomaki et al. 2009), as well as for assessing the benefits of conservation management for improving habitat quality in protected areas (Thomson et al. 2009). The main aim of this study was to use Zonation to identify sites with high forest connectivity; we examine the degree to which current PAs protect highly-connected areas of forest, and how effective proposed new PAs, including the proposed ‘Heart of Borneo’ PA, will be in this respect. The extent to which species perceive the landscape as connected or fragmented will depend on their dispersal ability, and so we varied the dispersal ability of species within Zonation to encompass a range of values that might be representative of different species in tropical forests. We do not intend these dispersal values to be exhaustive (for most taxa there is little information on dispersal ability, or the ability of animals to cross forest/non-forest boundaries; Benedick et al. 2007a), but rather to allow us to make general conclusions about the role of PAs to protect highly-connected forest.

Materials and methods

Data sources

We obtained data on forest cover for Borneo from a remotely-sensed global land cover data set (Global Land Cover 2000; http://bioval.jrc.ec.europa.eu/products/glc2000/products) at 30 arc second grid resolution (0.86 km^2). We extracted data for broadleaved and evergreen closed and open forest (subsequently termed ‘forest’), and all remaining land cover categories were designated as ‘non-forest’. There are currently no data on forest quality suitable for inclusion into the model, and so we assumed that all areas designated as ‘forest’ were of similar quality. However, these forest areas are highly heterogeneous, ranging from high-quality undisturbed forest within PAs, to highly-degraded production forest that has been logged repeatedly, and so will vary in their ability to support species diversity. Nonetheless, even heavily degraded forest is likely to be important for connectivity if it provides a closed canopy and suitable microclimates for forest-dependent species to disperse through the landscape. Data on the distribution of major towns and roads were obtained from Collins Bartholomew world digital map data (1: 5000000 scale), and the elevation of grid cells was obtained from a 30 arc second Digital Elevation Model (www.worldclim.org). Boundaries of existing PAs (IUCN categories), and proposed PAs (UNEP designated and Government approved sites) were extracted from the World Database on Protected Areas (WDPA; http://www.wdpa.org). The boundary of the proposed ‘Heart of Borneo’ protected area network was digitized from WWF (2005).

Zonation software

Zonation reserve-design software has been developed in order to identify sites important for conservation. In this study we used Zonation (Version 2.0; Moilanen and Kujala (2008)) to prioritize areas based solely on the extent of forest and proximity to other forest areas, and we did not include information on the distribution of species richness. Zonation considers the landscape as a grid of cells (0.86 km^2 grid resolution in this study), and prioritises cells by iteratively removing those cells whose loss causes the smallest marginal loss in the overall conservation value of the remaining landscape; those cells removed last are considered to have highest priority (Moilanen 2007). By this successive removal of low priority cells, Zonation ranked all cells on Borneo from 0 (worst) to 1 (best) in relation to forest extent and connectivity. We used the facility within Zonation to smooth the distribution of habitat with a two-dimensional kernel, where the width of the kernel can be considered as a measure of the dispersal ability of forest-dependent study organisms (Moilanen and Kujala 2008). Species' dispersal ability will affect habitat connectivity, and we assessed the degree to which our results were affected by species dispersal ability by altering the dispersal parameter (α) within Zonation. We examined effects of 1 km smoothing of habitat (default setting in Zonation; Moilanen and Kujala 2008), and also 5, 10, 15 and 20 km smoothing (i.e. Zonation $\alpha = 206.4$, 41.28, 20.64, 13.76, and 10.32 respectively; Moilanen et al. 2005; Moilanen and Wintle 2006), representing a range of different dispersal abilities. Many tropical species have limited dispersal ability, but we did not explore dispersal values less than 1 km. Zonation was run at $\sim$1 km grid resolution and so assigning species dispersal <1 km would not have allowed species to disperse out of grid cells and so would not have allowed us to study the role of connectivity. Thus, the results from our study are likely to apply to relatively mobile animal species.

There are four other option settings in Zonation, for which we used the default recommended settings; thus cells were removed according to the 'core-area' cell removal rule, and the 'warp factor' was set at 10 (i.e. the 10 worst cells were removed at each iteration) to maximise speed of analysis while maintaining reliability of output. In addition, we used the recommended default settings of 'edge removal' (i.e. cells were removed preferentially from the edges of forest areas), and 'add edge points' to prevent important areas being lost, and to keep computation times relatively short (Moilanen and Kujala 2008). Land cover data were categorical and included into Zonation as either 'forest' (category 1) or 'non-forest' (category 0). Areas of unsuitable habitat for species (urban areas and roads) were set as 'non-preferred' areas and so these cells were removed first (Moilanen and Kujala 2008).

Zonation output

We focused primarily on cells with Zonation ranks $\geq$0.9 i.e. the top 10% of cells with high connectivity (19% of forest habitat). We identified the locations of these highly-connected cells in relation to elevation on Borneo. In order to determine the degree to which PAs protect highly-connected forest, we quantified the percentage of cells with Zonation ranks $\geq$0.9 that occurred within existing and proposed PAs. We quantified the connectivity value of each PA based on the mean ranking of cells occurring within PAs, and examined whether mean Zonation rank of cells within PAs was correlated with PA area. All analyses were carried out in ArcGIS version 9.2. and R version 2.8.1.

Results

Location of highly-connected forest

Most of Borneo was historically covered with forest, but forest is now estimated to cover only 53% of Borneo (395,382 km^2; $N = 459{,}746$ grid cells). We focused on those cells

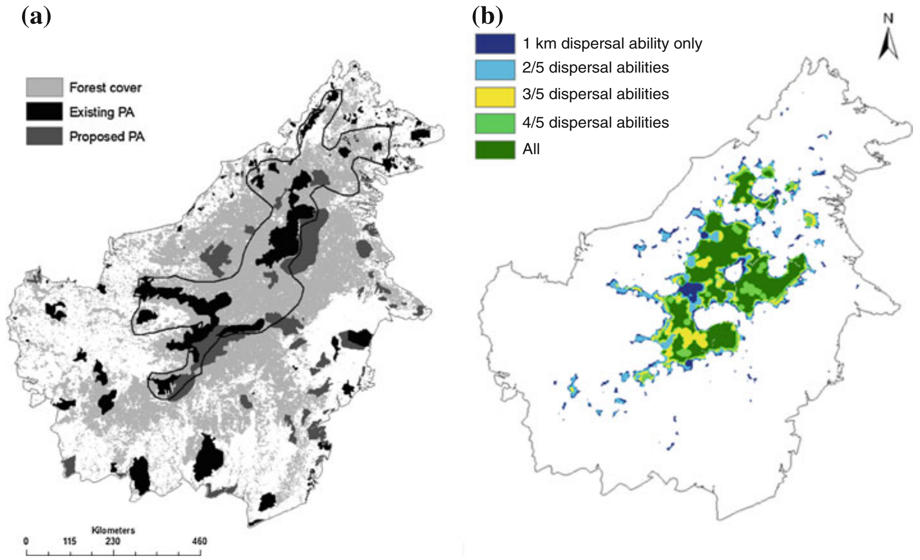

Fig. 1 The maps of Borneo show (**a**) locations of existing and proposed PAs, and distribution of forest cover on Borneo (from Global Land Cover 2000 for SE Asia), and (**b**) those cells with high connectivity (cells with Zonation rank score ≥0.9), and spatial overlap of these cells for different dispersal abilities (1, 5, 10, 15, 20 km). The *different shading* shows where increasing numbers of dispersal treatments (maximum of 5) overlap. The *solid black line* on panel (**a**) shows the boundary of the proposed 'Heart of Borneo' network of PAs

with the most highly-connected forest (i.e. cells with Zonation rank ≥0.9; $N = 86{,}601$ cells). Borneo still has large expanses of forest in its central montane region (Fig. 1a), and forest in this area has high habitat connectivity (Fig. 1b). A total of 64% (1 km dispersal treatment) of highly-connected forest cells occurred at higher elevation (above 400 m; Fig. 2a), and 20% of highly-connected forest cells were above 1,000 m. However, more than 60% of Borneo's land area occurs at low elevation below 200 m, although only 15% of highly-connected forest cells (1 km dispersal data) occurred in these low elevation areas (Fig. 2b). These findings were relatively insensitive to variation in species' dispersal ability (Fig. 2a); highly-connected forest occurred at higher elevation for all dispersal treatments (Fig. 2b) although these high ranked cells were more aggregated in the central zone of Borneo as dispersal ability increased (Fig. 1b). Examination of the spatial congruence of highly-connected forest according to different assumptions about species' dispersal abilities (Table 1) showed that overlap was high, especially when cells with Zonation rank ≥0.7 (i.e. top 30% of cells) were compared. The lowest degree of overlap was observed when comparing output for 1 and 20 km dispersal abilities. Because our findings were relatively insensitive to dispersal abilities, unless otherwise stated, we subsequently report in the main text only those findings for the 1 km dispersal treatment.

On Borneo, forest areas at high elevations have retained their integrity better than those at lower elevations. For example, our data show that only 11% of Borneo's total land area and 20% of its forest occurs above 600 m elevation, yet 37% of highly-connected forest cells, 33% of existing PAs, and 39% of the area of the proposed 'Heart of Borneo' PA occur above 600 m (Fig. 2). Thus whilst highland (>600 m) and montane (>1,000 m)

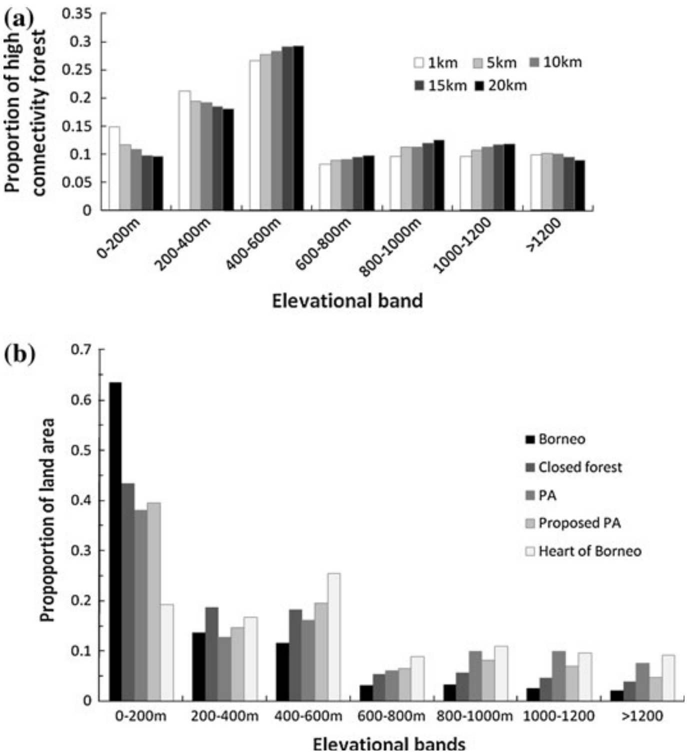

Fig. 2 The percentage of cells with (**a**) high connectivity (cells with Zonation rank score ≥0.9) in different elevation bands assuming different dispersal abilities, and (**b**) the percentage of cells in existing and proposed PAs, and proposed Heart of Borneo PA in different elevation bands. The total land area of Borneo in different elevation bands is also plotted

Table 1 Spatial overlap of cells with high connectivity (Zonation rank score ≥0.7 and ≥0.9) assuming different dispersal abilities of organisms (1, 5, 10, 15 and 20 km Zonation smoothing function)

	1 km	5 km	10 km	15 km	20 km
1 km		0.85	0.73	0.67	0.63
5 km	0.92		0.84	0.77	0.70
10 km	0.88	0.95		0.91	0.84
15 km	0.86	0.92	0.97		0.92
20 km	0.85	0.91	0.96	0.98	

The top triangle of values in the Table is for cells ranked ≥0.9, the bottom triangle for cells ranked ≥0.7. Data in Table show proportion overlap of treatment solutions using Zonation post-processing 'Solution Comparison' pairwise analyses

tropical forests constitute a relatively small area of Borneo, they are well represented in existing PAs and the 'Heart of Borneo' project. By contrast, >60% of Borneo's land area occurs at low elevation (<200 m), but only 43% of forest area, and 38% of existing PAs occur in these lowland forests. Thus our results highlight the need to protect more lowland forests.

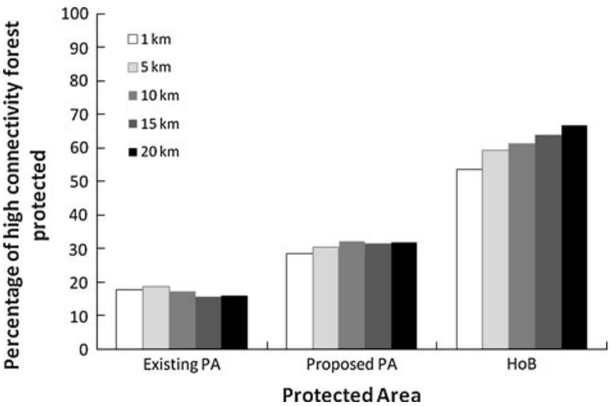

Fig. 3 Percentage of highly-connected forest (cells with Zonation ranked score ≥0.9) occurring within existing and proposed PAs, and the Heart of Borneo project

Protection of highly-connected forest

There are currently 177 PAs on Borneo, ranging in size from <0.86–12,000 km^2. Excluding the proposed 'Heart of Borneo' PA network, a further 43 separate PAs are proposed, spanning a similar range of sizes (1.7–12,000 km^2). A total of 18% of highly-connected forest cells occurs within existing PAs, but this value could potentially increase to 54% if all proposed PAs, including the Heart of Borneo, are protected (Fig. 3; details of PA size, location, IUCN category, and mean percentage of highly-connected forest cells occurring within PA boundaries according to dispersal treatments are listed in Supplementary Information (ST1)). However, even if these ambitious plans for proposed new PAs are implemented, 46% of highly-connected forest will remain unprotected. If none of the proposed new PAs are established, then >80% of highly-connected forest cells will not be protected.

There was a significant positive correlation between PA area and mean Zonation rank of cells (Spearman correlation, $r = 0.25$, $N = 177$, $P < 0.001$), indicating that larger PAs protect a greater proportion of highly-connected forest cells compared with smaller PAs. This pattern occurs because large PAs occur predominantly within the central montane region of Borneo, where extensive tracks of highly-connected forest persist (Fig. 1a).

Discussion

Protected areas are considered cornerstones of biodiversity conservation, yet only 9.1% of Borneo's land area is currently protected, falling short of the 10% target set by the Convention on Biological Diversity (Schmitt et al. 2009). Protected areas of Borneo are primarily in forested areas, although in many cases the forest within PAs has been logged and/or is highly degraded (Curran et al. 2004). In addition, large areas of remaining forest are not protected and our analyses showed that only 16–19% (depending on dispersal ability) of highly-connected forest (i.e. cells ≥0.9, which comprises 3–4% of total forest coverage) is protected. In tropical regions, preserving extensive tracts of undisturbed forests is crucial, however the preservation of forest corridors is also important for connecting remaining patches of remnant forest (Beier and Noss 1998). Most areas of forest on Borneo that are outside PAs are production forest and have been logged at least once, and are becoming increasingly degraded (Ashton 2008), and may not provide similar levels of connectivity as more pristine undisturbed habitats. Nonetheless, degraded and selectively logged forest on Borneo can support high levels of biodiversity (Berry et al. 2010; Edwards et al. 2011) and may provide important 'stepping stones' and 'corridors' linking more pristine habitats. Thus, the inclusion of degraded forest into our analyses may provide a better estimate of overall habitat connectivity than if we had considered only pristine forest habitat. However, these degraded habitats may become increasingly vulnerable to continued encroachment and further disturbance in future and need better management and protection; even highly degraded forest is likely to be more beneficial than plantations for the conservation of most species.

Output from Zonation indicated that Borneo still has a large expanse of highly-connected tropical forest located in the central montane region. These large areas are likely to support more species than smaller isolated fragments (MacArthur and Wilson 1963; Benedick et al. 2006) and may also be more capable of supporting mobile species which require extensive areas of habitat, such as Orang-utan (*Pongo pygmaeus*), Sumatran rhino (*Dicerorhinus sumatrensis*) and Bornean elephants (*Elephas maximus borneensis*). However, whilst iconic and critically endangered vertebrates are one conservation priority, their contribution to regional species richness is minimal compared with other taxa, which may have distributions elsewhere on Borneo. For example, highest tree diversity is at low elevation (<300 m), and high levels of dipterocarp endemism occur in low-lying areas in the North West geographical region on specific geological substrates (Ashton 2008, 2010), that are not part of the highly-connected forest areas identified by Zonation. Our primary aim was to investigate forest connectivity at a landscape scale and we did not consider species with very limited dispersal (i.e. <1 km) that fail to cross non-forest habitats. Land cover data suitable for our study were available only at a resolution of ~1 km grid and so inferring connectivity potential for species with dispersal abilities much lower than this would be difficult. However, if we assume that trends in connectivity in relation to dispersal continue beyond the range of values we investigated, then we can conclude that in general, organisms with greater dispersal abilities would be expected to benefit most from large areas of preserved habitat, while organisms with lower dispersal abilities might be better able to persist in smaller fragments of forest such as those scattered throughout the lowlands.

Our results indicated that even though large areas of forest have been converted to non-forest agricultural and urban areas, mid-elevation and montane forest integrity remains high, and these results were evident across a range of species dispersal abilities (1–20 km). These central regions support extensive tracts of forest because they are relatively remote and inaccessible, thus minimising anthropogenic disturbances, although this situation is likely to change in future with increasing pressure for land as human populations increase. By contrast, many areas of forest (including globally important hyper-diverse mixed dipterocarp forest) at low elevation are highly fragmented and relatively few PAs in these regions support highly-connected forest; for example PAs in South Kalimantan, Sabah and Brunei contain little highly-connected forest. There was reasonable consensus in terms of designation of high-connectivity cells in relation to different assumptions about species dispersal ability, although slightly more areas away from the central region were ranked highly with low (i.e. 1 km) dispersal ability.

Our findings suggest that existing PAs on Borneo are failing to protect most highly-connected forest areas. For example, Kinabalu Park in Sabah (northern Borneo; PA area = 767 km^2) contains the highest mountain in the Sundaland global biodiversity hotspot (Gunung Kinabalu, >4,000 m a.s.l.), and is an important centre of endemism, but this PA conserves relatively little highly-connected forest (mean Zonation rank = 0.62, SD = 0.14). Kinabalu Park PA is becoming increasingly isolated from other areas of forest because of widespread land-use change beyond the PA boundary in the past 50 years (Chen et al. 2009, 2011). Focussing conservation efforts into reducing the isolation of this PA may be an effective use of conservation resources for preventing loss of biodiversity in this UNESCO World Heritage site.

Inclusion of species distribution data

Our analyses focussed solely on availability of forest habitats because we were interested in quantifying generic forest connectivity. Nonetheless, PAs are designated for many reasons, not only in relation to conserving habitats but also the species these habitats support. In tropical regions, observation data on distributions of species are often lacking, of poor quality, or focussed on just a few iconic species. Several tropical studies have modelled species distributions in relation to environmental variables (climate and habitat) in order to project distributions at finer spatial resolution (e.g. Kremen et al. 2008). These analyses have demonstrated the role of habitat in limiting species distributions. For example, Beck et al. (2011) highlighted the importance of forest in predicting moth diversity on Borneo, and revealed very similar conclusions to those presented in this study in terms of locations of high priority sites in the forested central regions of Borneo. Given that studies have shown that good locations for conserving diversity of one taxon are not effective for other taxa (Kremen et al. 2008), and that tree species richness is a reasonable proxy for overall biodiversity (Ashton 2008, 2010), including arthropods (Novotny et al. 2002), studying the availability of forest per se is likely to be a cost-effective, rapid proxy for the distribution of tropical biodiversity. However, focusing conservation effort into preserving large areas of intact forest may fail to conserve all species within a region (Benedick et al. 2006). This is especially pertinent on Borneo where coastal forest remnants, especially in the north-west, support high levels of plant species richness and endemism of global significance (Ashton 2010), and thus where focussing on conserving forest connectivity will fail to preserve these restricted-range species. However, in other tropical regions, the loss of large vertebrate predators from forest fragments results in trophic cascades that have detrimental impacts on seedling recruitment within forest remnants (Terborgh et al. 2001), supporting the notion of conserving large tracts of forest. Thus, we argue for the inclusion of measures of habitat connectivity, together with species richness and endemicity, into assessments of conservation value of sites.

There is increasing recognition that PAs not only need to protect the current distributions of species, but also conserve species that may change their ranges in future under climate change (Hannah 2010). There is on-going debate about the best ways of designing landscapes that are likely to be most effective at conserving species (Green et al. 2005; Edwards et al. 2010), and landscape designs that best preserve static distributions may not be the same as those best for conserving dynamic distributions (Hodgson et al. 2009, in press). In our study, many areas at low elevation have been converted to oil palm plantations, and remaining remnants of forest in these areas are increasingly fragmented and dispersal among forest remnants is restricted by an inhospitable surrounding agricultural matrix. Improving the matrix, as well as increasing the quality and quantity of forest habitats may increase habitat connectivity. Methods for the sustainable production of palm oil and timber include recommendations for riverine forest strips to reduce soil erosion (Round table for Sustainable Palm Oil (RSPO) 2006), which might also provide dispersal corridors if such recommendations were enforced and implemented (Pescott et al. 2010).

Heart of Borneo

The designation of 51,413 km^2 of proposed PAs (not including the Heart of Borneo) potentially increases the extent of high connectivity forest protected by 8,170–12,040 km^2, representing 29–32% of highly-connected forest sites. The majority of these new PAs cover centrally situated lowland forest and in several cases are adjacent to existing PAs. They therefore offer greater protection to larger, more wider ranging species than do existing PAs, however they still leave ~70% of well-connected forest unprotected. The Heart of Borneo project could potentially increase the extent of high-connectivity forest that is protected to 54–67% (almost doubling the extent of protection potentially offered by proposed PAs alone). The trans-boundary 'Heart of Borneo' project already includes some of the largest PAs with the highest concentrations of highly-connected forest in Borneo and would include a large component of Borneo's biodiversity and species richness. The project does also include intervening non-forest areas, and schemes to link existing PAs and improve the quality of matrix might be feasible under the scheme. Thus the Heart of Borneo is well-placed to protect many remaining forest areas of high connectivity in central sub-montane and montane regions. Output from reserve-design software such as Zonation could also be used to refine the precise location of the boundary of the Heart of Borneo to ensure it is best-placed to include forest areas of high connectivity.

Conclusions

Conserving areas of high habitat connectivity, and the populations and ecosystem services within them, is perhaps the most effective way to facilitate adaptation of species to changing environmental conditions. Zonation reserve design software enables forest connectivity to be assessed and areas of high connectivity prioritized. In this study, we used Zonation to identify highly-connected forest areas across the entire Borneo land mass, but Zonation could also be applied in future at smaller spatial scales to identify the most highly-connected forest areas within a particular political region where conservation actions may be more likely to be implemented in the immediate future. Our study has shown that there are still areas of Borneo's tropical rainforests that have retained their integrity, but these areas are located in central Borneo, and many lowland and coastal areas of forest that support high species richness and endemism are unprotected and becoming increasingly isolated within agricultural landscapes. Improving forest connectivity through reforestation and rehabilitation of degraded forest may be required to maintain populations of forest species in these PAs in future.

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