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Conserving biodiversity in production landscapes

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Abstract. Alternative land uses make different contributions to the conservation of biodiversity and have different implementation and management costs. Conservation planning analyses to date have generally assumed that land is either protected or unprotected and that the unprotected portion does not contribute to conservation goals. We develop and apply a new planning approach that explicitly accounts for the contribution of a diverse range of land uses to achieving conservation goals. Using East Kalimantan (Indonesian Borneo) as a case study, we prioritize investments in alternative conservation strategies and account for the relative contribution of land uses ranging from production forest to well-managed protected areas. We employ data on the distribution of mammals and assign species-specific conservation targets to achieve equitable protection by accounting for life history characteristics and home range sizes. The relative sensitivity of each species to forest degradation determines the contribution of each land use to achieving targets. We compare the cost effectiveness of our approach to a plan that considers only the contribution of protected areas to biodiversity conservation, and to a plan that assumes that the cost of conservation is represented by only the opportunity costs of conservation to the timber industry. Our preliminary results will require further development and substantial stakeholder engagement prior to implementation; nonetheless we reveal that, by accounting for the contribution of unprotected land, we can obtain more refined estimates of the costs of conservation. Using traditional planning approaches would overestimate the cost of achieving the conservation targets by an order of magnitude. Our approach reveals not only where to invest, but which strategies to invest in, in order to effectively and efficiently conserve biodiversity.

Key words: biodiversity; conservation planning; Indonesia; opportunity costs; production forest; protected areas.

Introduction

The conversion of tropical forests is a considerable threat to biodiversity in South East Asia (Whitmore and Sayer 1992), where deforestation rates rank amongst the highest in the world (Achard et al. 2002, Sodhi et al. 2004). The annual rate of deforestation in Indonesia in the 1990s was 1.8 million hectares per annum, or approximately 2 percent per annum (Holmes 2000, Forest Watch Indonesia and Global Forest Watch [FWI/GFW] 2002, Food and Agriculture Organization [FAO] 2006). The protected area estate is extensive in South East Asia, 18.6 percent of Indonesia's forests, for example, are designated for the primary purpose of conservation (FAO 2006). But there is evidence that this system of protected areas will not ensure the persistence of biodiversity (Jepson et al. 2001, Curran et al. 2004, DeFries et al. 2005, Steinmetz et al. 2006, Dutton et al. 2009). In Kalimantan (Indonesian Borneo), two-thirds of forest loss between 1997 and 2002 took place in proposed or existing protected areas (Fuller et al. 2004). The main constraints on the performance of protected areas in the region include inadequate resources for management, variable levels of governance and community support, competition from other land uses, the opportunity costs of protection, and global demand for tropical timber (Bruner et al. 2001, Dutton 2001, Jepson et al. 2002).

Besides strictly protected areas, Indonesia's forests occur in a diversity of land uses ranging from production to watershed protection, with some areas cleared or pending conversion to other land uses. Each

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FIG. 1. Location of East Kalimantan on the island of Borneo.

of these land uses contribute differently to the conservation of biodiversity and has different costs associated with its initial implementation and ongoing management. Some land uses (such as a well-managed protected area of primary forest) provide habitat for all original species, along with a diversity of food sources, but may provide little economic return (Meijaard et al. 2006, Nakagawa et al. 2006, Wells et al. 2007, Meijaard and Sheil 2008). Other land uses (such as palm oil plantations) are more restricted in their provision of habitat with the resultant mammal diversity reflecting these differences (Fitzherbert et al. 2008, Danielsen et al. 2009). Across all land uses there emerge unique opportunities for conservation beyond strictly protecting forest.

While well-managed logging concessions can deliver significant benefits for the conservation of moderately sensitive biodiversity, a limited proportion of Indonesia's forests present such opportunities because much forest is degraded or harvested (FWI/GFW 2002). More than half of Indonesia's forests have been allocated to timber production (54 million hectares) and a further two million hectares of industrial wood plantations have been established (FWI/GFW 2002). The majority of these forests occur in concessions that are owned by the government and for which the use rights are often "leased" to commercial operators (Dennis et al. 2008). These concessions were established to facilitate long-term timber production (Meijaard et al. 2006), but in some cases have led to illegal logging, and conversion to other land uses (Jepson et al. 2001). In 2001, nearly 30% of a sample of surveyed logging concessions in Indonesia were reported to be in a degraded condition (FWI/GFW 2002). Furthermore, it is estimated that despite ostensible government regulation, more than half of Indonesia's wood supply is obtained from illegal logging (Obidzinski et al. 2007). The impact of unsustainable timber extraction on biodiversity is further exacerbated by the impact of forest fires, with the two processes inextricably linked (Dennis et al. 2005, Dennis and Colfer 2006). Conversion of forest to a timber plantation or an estate crop plantation, such as oil palm (*Elaeis guineensis*), represents long-term consequences for its potential contribution to biodiversity conservation (FWI/GFW 2002, Meijaard and Sheil 2007*b*).

In production landscapes there are a range of land uses and conservation strategies that can potentially contribute to meeting biodiversity conservation goals. Such strategies include developing compensation mechanisms for setting aside high conservation value forest areas within timber concession areas, reduced impact logging practices, and improved management of existing protected areas. Recent theoretical and technical developments in the field of systematic conservation planning have moved beyond consideration of the landscape or seascape as binary (involving only protected areas and an unprotected matrix) to prioritizing investments in multiple conservation strategies across a variety of land uses (Wilson et al. 2007, Watts et al. 2009). This approach allows the varying sensitivity of biodiversity to land use change and modification and the importance to biodiversity conservation of areas that are not formally protected to be accounted for. We choose East Kalimantan as a case study, because it represents one of the most species-rich areas in the world (Myers et al. 2000, Brooks et al. 2006), but has a rapid rate of land use change and concomitant high threats to forest species. The aim of this research is to develop and apply a new approach to conservation planning that explicitly accounts for the contribution of a diverse range of conservation strategies, which vary in cost and also benefits, to achieving conservation goals. We compare our approach to traditional planning approaches which account only for the contribution of protected areas or the opportunity costs of conservation to the timber industry.

METHODS

Study region

East Kalimantan is the largest of four provinces in Indonesian Borneo (covering approximately 229 855 km^2; Fig. 1). Its tropical forests range from lowland to montane forest to swamp and mangrove forest. East Kalimantan supports more than 170 forest-dwelling mammal species, with 39 classified as threatened in the IUCN Red List (IUCN 2008; Appendix: Table A1). Despite their globally recognized conservation importance and relatively high level of protection (20% of East Kalimantan is protected [WDPA Consortium 2004]), the

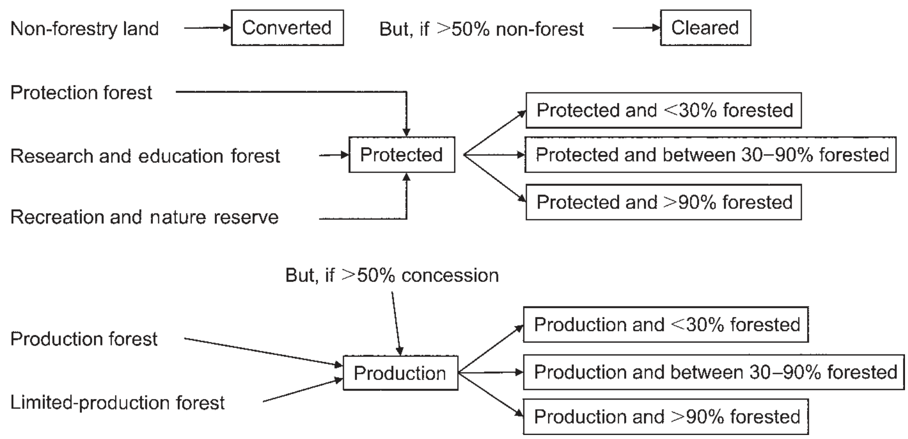

FIG. 2. Derivation of the land use zones in East Kalimantan.

forests of East Kalimantan are threatened by commercial logging, palm oil and timber plantations, mining, agricultural development, and forest fires (Sodhi et al. 2004).

Analysis framework: Marxan with Zones

We employ a multiple land use planning version of the decision-support tool Marxan (Possingham et al. 2000). Marxan is an area selection algorithm that aims to identify planning units (the spatial units of analysis) that are important for protection given their cost-effective contribution to achieving biodiversity targets (Ball et al. 2009). Within the revised formulation of Marxan, termed "Marxan with Zones" (Watts et al. 2009), the number of land use zones in which a planning unit can be placed is expanded. Marxan has one static cost, the cost of making any planning unit a protected area. In contrast, the cost in Marxan with Zones is that of implementing a particular conservation strategy in a specific land use zone.

Our application of Marxan with Zones to conservation planning in East Kalimantan requires information on land uses and conservation strategies and the cost of implementing these strategies. It also requires information on the distribution of biodiversity, conservation targets, and the contribution of each land use to achieving these targets.

Land use zones

We use a combination of land use, concession status, and forest cover to classify forest into eight land use zones (Fig. 2). We delineate our planning units using the national land use classification system developed by the Indonesian Forestry Ministry of Indonesia, the Forest Use Consensus and Synchronization of Provincial Spatial Planning. This classification system identifies six broad land use classes and we simplify these to "cleared," "converted," "protected," and "production." For production and protected forest we classify each planning unit into one of three categories of forest cover (1) less than or equal to 30%, (2) between 30% and 90%, and (3) greater than or equal to 90% (Fig. 2). We assume that primary forest has 100% forest cover. We delineate 4546 planning units classified according to land use and based on a 10 × 10 km grid (reflecting the resolution of the spatial data employed in the analysis; Fig. 3).

Species distribution data and targets

We employ mammal distribution data compiled as part of the South East Asian Mammal Databank project (SAMD; Catullo et al. 2008). The SAMD database contains information on the distribution (extent of occurrence and area of occupancy) of 1086 mammal species (database *available online*).[9]

Deductive distribution models, available for 901 species, were constructed using information on species–habitat relationships and environmental data. For each species a synthetic suitability index was constructed identifying areas of suitable land cover within the known elevation range and also inside the species' extent of occurrence (Catullo et al. 2008). The suitability of habitat for each species is ranked as high, medium, low, unsuitable, and unknown. The SAMD database represents the most comprehensive species dataset available for the study region, although area of occupancy maps are likely to contain errors of omission and commission (Rondinini et al. 2006).

Catullo et al. (2008) tested the predictive ability of 21% of the distribution models, a sample representative of the species within the entire dataset. The level of agreement between each model and independently collected species presence data was measured and the models were also compared to a set of random data points (statistical significance was measured using a permutation test over 1000 replicates). In 74% of the cases the agreement between the distribution models and the points of presence was higher than expected by

[9] ⟨www.ieaitaly.org/samd⟩

chance, while for only eight species the agreement was significantly lower.

We identify 170 forest dwelling mammals that occur in East Kalimantan and use the SAMD database to determine the area of occupancy of each species based on the areas classified as high habitat suitability (Appendix: Table A1). We use a new method for setting conservation targets for each species that aims to deliver equitable targets across all species, rather than employ uniform targets (Miller and Sammuto 1983, Lande 1993, McCarthy et al. 2005, Carwardine et al. 2009). The targets aim to achieve equitable protection of each species by employing information on the life history characteristics. The resultant target area was then modified by the home range size and area of occupancy of each species.

From Lande (1993) (and see also McCarthy et al. 2005), we know that the mean time to extinction (M) for a single population exposed to environmental stochasticity can be approximated by the following formula:

$$M = \frac{2K^b}{\sigma^2 b^2} \qquad (1)$$

where K is the carrying capacity of the population, σ^2 is the variance in the growth rate of the population, b is a constant and is calculated via ($[2r/\sigma^2] - 1$) (McCarthy et al. 2005), and r is the intrinsic mean growth rate of the population. If we assume that $M = 100\,000$ years is an approximate mean time to extinction for every species, then a target population size, K, can be obtained via rearranging Eq. 1:

$$K = \left(\frac{100\,000\sigma^2 b^2}{2}\right)^{1/b}. \qquad (2)$$

In general, data on r and σ^2 are unavailable. Sinclair (1996) found the maximum instantaneous rate of growth of a population of mammals over a year (r_m) to be approximated by a function of the body mass via $r_m = 1.375W^{-0.315}$, where W is the adult live body mass of females in kilograms. Sinclair (1996) also found the instantaneous rate of change between censuses, r_t, to relate to body mass via $r_t = 0.805W^{-0.316}$, with r_t approximated by r_m/T, with T calculated according to $1.74W^{0.27}$ (Miller and Sammuto 1983). We use these approximations for r_t and σ^2 to calculate b and we substitute these values into Eq. 2 to derive K.

We multiply the resultant target population size by the home range of each species to obtain the target area. Since this assumes that the full target for each species will be met within the study region (even if it occurs outside the study region) we adjust the target by the percentage of the area of occupancy in Borneo that lies within East Kalimantan (Appendix: Tables A1 and A2). As our conservation strategies do not allow for the restoration of habitat, we reduce the target for 34 species to their area of occupancy in East Kalimantan, as the target of these species exceeded the area of occupancy. In order to account for the variable contribution of each land use zone to target achievement, we calculate the contributing area of occupancy. This allows the maximum possible zone contribution given the allowable land use transitions to be determined (see Table 1, with the allowable land use transitions outlined below). We reduce the target to the contributing area of occupancy for 41 species for which the target exceeded the contributing area of occupancy (Appendix: Table A2).

We explore the sensitivity of our targets (and the overall results) to the home range data as this was the variable for which we have least documented information. We increase and decrease the home range by an order of magnitude and recalculate our targets (Appendix: Table A2).

Land use transitions and conservation strategies

We establish the following rules for possible land use zone transitions and conservation strategies within the planning analysis:

1) Since we are not considering restorative activities and are taking only a short-term view of the forested landscape, the percent forest cover of a planning unit cannot be improved.

2) Planning units that are already cleared and converted cannot change zones.

3) Production or protected forests cannot be cleared or converted, and the percent forest cover cannot be modified.

4) Protected planning units cannot change zones, although the management of these planning units can be improved, which will impact species differently.

5) Production planning units can be protected, or alternatively logging practices and the management of these planning units can be improved, and this will impact species differently.

Contribution of each land use zone to conservation

Alternative land use zones differ in both the intensity of disturbance and the recovery time after disturbance. The "zone contribution value" employed in Marxan with Zones varies between 0 and 1. For example, if the contribution of a zone is 1, then each hectare of habitat will contribute one hectare toward the target for this species in this zone. If the zone contribution is 0.6, then each hectare of habitat would contribute 0.6 ha toward the target for this species in this zone.

We develop species-specific contributions of each land use zone by classifying each forest-dependent species occurring in the study region into three categories: low, medium, and high sensitivity to extractive land use as derived from the scientific literature and expert opinion (Appendix: Table A1). For species of low sensitivity we allow the target to be met across all land use zones, with the exception of the cleared forest zone. For species of medium sensitivity we allow the target to be met across uncleared and unconverted zones with at least 30%

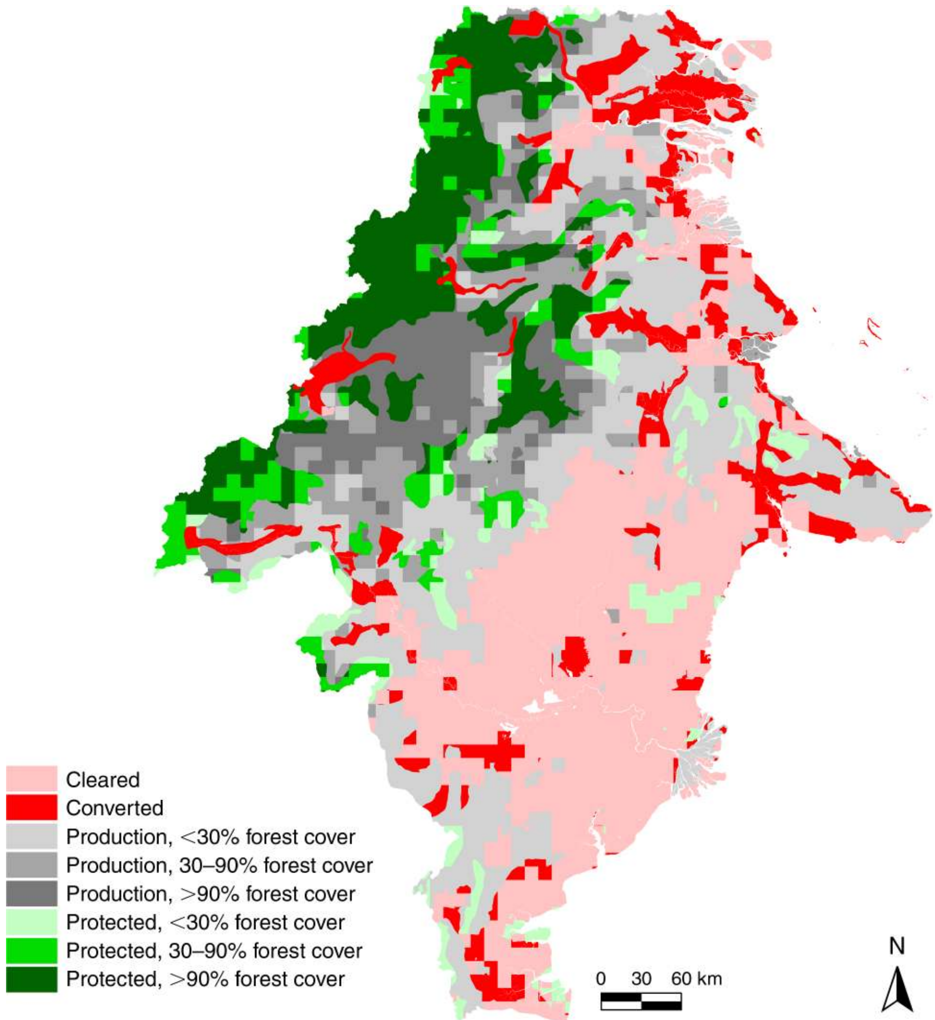

FIG. 3. Current land use zones in the Indonesian province of East Kalimantan.

TABLE 1. An example of target contributions of each land-use zone given the relative sensitivity of three species of mammal to forest loss and degradation.

Land use	Percentage of target contribution		
	Plantain squirrel (low sensitivity)	Lesser mouse-deer (medium sensitivity)	Bornean gibbon (high sensitivity)
Cleared	0	0	0
Converted	0.1	0	0
Production, <30% forest cover	0.1 (0.25)	0	0
Improved production, <30% forest cover	0.1 (0.25)	0	0
Production, between 30 and 90% forest cover	0.1 (0.5)	0	0
Improved production, between 30 and 90% forest cover	0.25 (0.5)	0	0
Production, >90% forest cover	0.25 (1)	0.25 (1)	0.25 (1)
Improved production, >90% forest cover	0.5 (1)	0.5 (1)	0.5 (1)
Protected, <30% forest cover	0.1 (0.25)	0	0
Improved protection, <30% forest cover	0.25 (0.25)	0	0
Protected, between 30 and 90% forest cover	0.25 (0.5)	0.25 (0.5)	0
Improved protection, between 30 and 90% forest cover	0.5 (0.5)	0.5 (0.5)	0
Protected, >90% forest cover	0.5 (1)	0.5 (1)	0.5 (1)
Improved protection, >90% forest cover	1 (1)	1 (1)	1 (1)

Notes: The values in parentheses indicate the maximum possible zone contribution given the allowable zone transitions, which was used to calculate the contributing area of occupancy for each species. The plantain squirrel (*Callosciurus notatus*) has low sensitivity to forest degradation; the lesser mouse-deer, also known as the lesser Indo-Malayan chevrotain (*Tragulus kanchil*), has medium sensitivity; and the Bornean gibbon (*Hylobates muelleri*) has high sensitivity.

TABLE 2. Cost per hectare (in US$) of each conservation strategy.

Cost component	Establishment of new protected areas	Improved management of production forest	Improved management of protected areas
Start up costs	50	60	
Management costs	163		163
Opportunity costs	2634		
Total	2847	60	163

forest cover. For species of high sensitivity we allow the target to be met in zones with greater than 90% forest cover. These contributions are assigned on the basis that species that are highly sensitive to forest loss and degradation will require greater forest cover and the fractions are assigned to each land use class in an internally consistent manner. An example of this procedure for three species of mammals is provided in Table 1.

Costs of each conservation strategy

We determine the cost of each conservation strategy from the perspective of a conservation agency. We assume there to be no cost to stay in the current land use. However, there is a cost to change a planning unit from production to protected status, or to improve the management of production or protected forest. Table 2 outlines the types of cost (start-up, management, and opportunity costs) that apply to each conservation strategy, which are applied uniformly across the study region. Most start-up costs represent an up-front cost, whereas management and opportunity costs can represent ongoing annual costs. We endow the ongoing costs for 30 years and assume an inflation rate of 3.7% and an interest rate of 4.4%. For example, management costs represent a per annum cost of US$6 per ha estimated from The Nature Conservancy operating budgets from the region, and when endowed over 30 years represent an upfront cost of US$163 per ha.

In our analysis, changing a production forest to a protected forest assumes no extractive use, and will be associated with an opportunity cost, in addition to start-up and management costs. We calculate the former from the estimated profit in the year of extraction (Venter et al. 2009), and endow this cost over 30 years. Maintaining and improving the management of an already protected forest will incur the costs of management (but no start-up or opportunity costs). We represent the improvement in management of production forests by the costs associated with reduced impact logging. Holmes et al. (2000) and van Gardingen et al. (2003) found that reduced impact logging does not incur an opportunity cost as it can yield more timber and incur lower harvesting costs. We account for the cost of training concession operators every five years in reduced impact logging practices (estimated to equate to US$11 per ha; Applegate 2002), and we endow this cost over 30 years. We explore the sensitivity of our results to the cost data by doubling and halving the baseline cost for each conservation strategy.

Scenarios

We compare four scenarios. Scenario 1, termed the full zoning analysis, was formulated using the data outlined above. The conservation strategies explored in the full zoning analysis represent the maintenance of the status quo or the improved management of the system either through reduced impact logging, the creation of new protected areas, or the improved management of existing protected areas. For Scenario 2, we considered only the potential to convert production forest to protected areas or to improve the management of existing protected areas (that is, we limit our strategies to those associated with protected areas and do not consider the option to improve the management of production forest). The same targets as the full zoning analysis were employed and the contribution of production forest to meeting these targets was acknowledged. This scenario was established to investigate the impact of not considering the full diversity of available conservation strategies at our disposal. Scenario 3 is a modification of Scenario 2 but only protected forest is considered to contribute to meeting the species targets and our species targets were the full targets (i.e., they were not modified to account for the contributing area of occupancy according to the allowable zone transitions). This scenario reflects widespread assumptions in conservation planning and biogeography: the conservation strategy is limited to protected area establishment and only protected areas contribute to meeting conservation targets. It reflects a binary approach to conservation planning (as it ignores the potential contribution of non-protected land uses). For Scenario 4, we modify the full zoning analysis so that the costs of each conservation strategy are considered equal and represented by the opportunity costs of conservation (i.e., US$2634 per ha). Scenario 4 is used to investigate the effects of using simplistic opportunity cost as the measure of the cost of conservation.

RESULTS

We discover that under our full zoning analysis (Scenario 1) we could achieve many of the targets in East Kalimantan by establishing new protected areas in only 143 190 ha of forest, located near the borders with Sabah and with South and Central Kalimantan. These

Table 3. Recommended changes in the land use zone configuration in East Kalimantan, Indonesian Borneo, under the full zoning analysis.

Land use zones	Current area of each land use (ha)	Recommended area under the full zoning analysis (ha)
Cleared	5 714 366	5 714 366
Converted	2 105 111	2 105 111
Production, with less than 30% forest cover remaining	4 469 618	4 429 808
Improved production, with less than 30% forest cover remaining	0	0
Production, with between 30 and 90% forest cover remaining	918 610	33 620
Improved production, with between 30 and 90% forest cover remaining	0	872 641
Production, with greater than 90% forest cover	2 278 120	137
Improved production, with greater than 90% forest cover	0	2 186 951
Protected, with less than 30% forest cover remaining	835 808	182 190
Improved protection, with less than 30% forest cover remaining	0	693 429
Protected, with between 30 and 90% forest cover remaining	710 865	15 025
Improved protection, with between 30 and 90% forest cover remaining	0	708 188
Protected, with greater than 90% forest cover	2 513 334	0
Improved protection, with greater than 90% forest cover	0	2 604 365
Total area	19 545 832	19 545 832

areas (which comprise 60 planning units) contribute to the representation on average of 110 species per planning unit, whereas the average contribution for each planning unit in the study region is 88 species. The frequency with which these planning units are classified as a protected land use zone is 100%, meaning that if they are not protected then one or more species will be unable to meet their targets. The planning units on the border with Sabah, for example, represent the handful of planning units in East Kalimantan which contains the Asian elephant (*Elephas maximus*).

The results of Scenario 1 also reveal that in order to cost-effectively meet the prespecified targets, while accounting for the relative sensitivity of mammalian fauna to land use degradation, the area under improved management must increase substantially (Table 3). Planning units that have a higher forest cover were favored for improved management, reflecting the higher contribution to target achievement of these planning units. The land use design from the full zoning analysis is estimated to cost approximately US$1.22 billion to establish and manage over the next 30 years (Fig. 4).

For some species we were unable to completely meet the targets. Under the full zoning analysis, the average proportion of the targets achieved was 0.96. The minimum proportion of the target met for a species was 0.62 for the Least Horseshoe Bat (*Rhinolophus pusillus*). This species is common and widespread and considered to have low sensitivity to forest degradation, and has been found to roost in human habitations. Nonetheless, extensive forest conversion within the range of this species in East Kalimantan makes the achievement of its target difficult. This is despite all land uses being considered to contribute to the target. Bats in general, for similar reasons, were among the species for which target achievement was most difficult. There are 10 species of bat with less than 70% target achievement under the full zoning analysis.

We compare the full zoning analysis (Scenario 1) to Scenario 2, where only the conversion of production forest to protected forest and the improved management of existing protected areas are considered. Under Scenario 2, the land use plan required to meet the pre-specified targets in a cost-efficient manner is estimated to cost US$7.7 billion to establish and manage over the next 30 years (Fig. 4). In Scenario 3, the only land use considered to contribute to the targets is protected areas, and the estimated cost of the plan is US$19 billion to establish and manage over the next 30 years (Fig. 4). We also compare the full zoning analysis (Scenario 1) to Scenario 4, which makes the simplistic assumption that the costs of conservation are equal across all possible zone transitions and equates to the opportunity costs of conservation to the timber industry. Under this scenario, the estimated overall cost of the resulting land use plan would be $7.5 billion over the next 30 years (Fig. 4). The true cost of this plan (using the cost of each conservation strategy employed in Scenario 1 as the measure of truth) would be approximately US$2.9 billion.

Our overall results were insensitive to the home range employed to create the targets and the baseline cost of

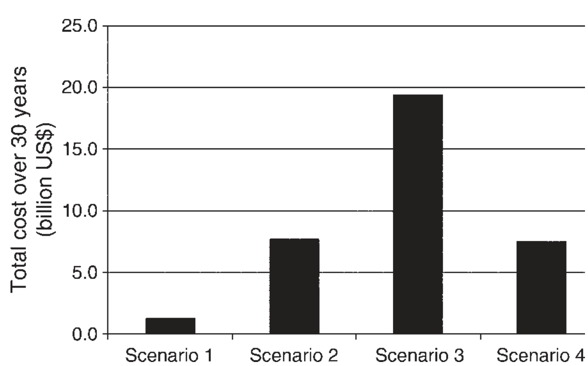

Fig. 4. Cost of the land use plans derived under each scenario (see *Methods: Scenarios* for descriptions).

each conservation strategy. Under each sensitivity analysis, Scenario 1 consistently outperformed the other scenarios in terms of overall cost and level of target achievement. If our home ranges were incorrect by an order of magnitude (either underestimated or overestimated) then the cost of the land use plan associated with Scenario 1 would range from US$918 million to US$3.8 billion over 30 years, respectively. If our baseline costs were halved or doubled, then the cost of the land use plan associated with Scenario 1 would be US$1.8 billion to $US3.6 billion over 30 years, respectively.

Discussion

Our analysis is an important step towards the development of an integrated plan for biodiversity conservation in East Kalimantan. We provide a new conceptual framework for conservation planning that has general applicability in production landscapes, have developed a baseline database to support such analyses, and pioneer the application of a new decision support tool that explicitly accounts for the contribution of a variety of land uses and conservation strategies. Our analysis suggests that an additional 143 190 ha of new protected areas is required to achieve the prespecified mammal targets and illustrates the potential contribution of the improved management of large areas of production forest and existing protected areas. In a recent gap analysis of East Kalimantan's reserve system using the SAMD database, Drummond et al. (2009) found that several mammalian megafauna are afforded only minimal protection, including the Asian elephant and Bornean orangutan (*Pongo pygmaeus*). Drummond et al. (2009) accounted only for the development of new protected areas, and recommended up to a fivefold increase (an addition of between 7 and 10.4 million ha) to the current protected area system. Moore et al. (2004) recommended doubling the current reserve system in East Kalimantan. A substantial increase of the protected area estate in East Kalimantan is however unlikely to be achievable in a country where the establishment of new protected areas is considered a low priority by government authorities (Jepson et al. 2002).

Rautner et al. (2005), Jepson et al. (2002), and Slik et al. (2009) argue for increasing protection of the highlands bordering Kalimantan and Sarawak. Our analysis found priority areas for protected area establishment in East Kalimantan to be located near the border with Sabah and along the southern border of the province. This follows earlier recommendations by Jepson et al. (2002) to protect the area bordering Sabah, a proposal that has not been implemented because of the significant potential for oil palm development in this relatively flat area which is accessible to Sabah's extensive infrastructure. Such realities of planned land use developments in East Kalimantan reveal the importance of modifying our analyses to account for the threats and opportunities to conservation in the province (Wilson et al. 2005, Knight and Cowling 2007, Murdoch et al. 2007). Future research must expand our analysis to account for the increased opportunity costs in this region, to understand the magnitude of biodiversity loss if this area is not conserved, and to generate alternative strategies if extensive oil palm development near Sabah cannot be altered.

The effective and sustainable management of the unprotected matrix is essential in East Kalimantan given the large proportion of remaining forests that are classified as production and used for timber harvest (Sist et al. 2003, Meijaard et al. 2005, Meijaard and Sheil 2007*b*). We estimate that the equitable protection of mammal species through improved land management will cost US$1.22 billion over the next 30 years (or US$108 million per annum if we assume the costs are incurred on an annual basis). The current total investment in protected area management (just one of the strategies we considered) across all of Indonesia equates to approximately US$55 million per annum, and is thought to reflect a shortfall of US$82 million in order to achieve optimal management (McQuistan et al. 2006). The contribution to biodiversity conservation of reduced-impact logging, which is increasingly recognized as a sustainable land use management option that has the potential to deliver both social and environmental outcomes with minimal costs to the timber industry (Holmes et al. 2000, van Gardingen et al. 2003), was accounted for in our analysis.

The estimated cost of the land use plan from the full zoning analysis (Scenario 1) is substantially less than the estimated cost of US$7.7 billion over 30 years (or US$690 million per annum) to achieve the same targets through only the establishment and improved management of protected areas (Scenario 2). If we completely ignore the contribution of production forest to achieving our targets (Scenario 3) then the estimated cost will be US$19 billion over 30 years (or US$1.65 billion per annum), comprising a recommended increase in the protected area estate by 6.8 million hectares. Accounting only for the contribution of protected areas would therefore overestimate the required expenditure by 15 times, and the area requiring protection by almost 50 times. This reveals the potential costs of a binary perspective in conservation planning and the economic and ecological imperative of considering the contribution of the unprotected matrix in conservation planning analyses. Most conservation planning analyses are structured in a similar way as Scenario 3 (assuming land is either protected or unprotected and no contribution from the unprotected estate) and are therefore likely to deliver pessimistic estimates of the costs of achieving our conservation goals, and similarly a conservative estimate of the level of goal achievement.

If we had assumed that the actual costs of conservation were simply defined by the opportunity costs of conservation to the timber industry (Scenario 4), then the estimated costs of delivering our conservation outcomes would be increased by seven times. This is because some conservation strategies, such as improved logging techniques, do not require the logging industry to forgo their revenue and others, such as improved management of protected areas, occur in areas where industries cannot legally access resources. Opportunity costs are a commonly used metric of the costs of conservation (Naidoo and Adamowicz 2006, Naidoo and Iwamura 2007, Carwardine et al. 2008*a*). Our results illustrate a need for caution in the use of a simplistic opportunity cost measure as a generic cost surrogate and the importance of identifying and employing the cost surrogate that most closely reflects the planned conservation strategy (Carwardine et al. 2008*b*). This shortcoming is revealed by our analysis as it accounts for the differential costs of a range of conservation strategies.

While we accounted for the differences in costs between conservation strategies, these costs were assumed to be homogenous across the study region. This assumption was necessary due to a lack of spatially explicit cost data. The impact of this is that we have likely overestimated the costs of conservation as the costs employed assume the full start-up, management, and opportunity costs for implementing each conservation strategy in each planning unit. Overestimating the costs of conservation may induce a lack of public and political support for conservation strategies for which the costs appear overinflated, potentially resulting in the perception that conservation is an economically and socially unfeasible option. We found our performance assessment of the different scenarios to be insensitive to the baseline cost employed, although we hope to explore options to incorporate the spatial heterogeneity in the costs of different conservation strategies in the near future.

The varying contribution of each land use zone to the conservation targets employed in our analysis account for the relative sensitivity of the mammals to forest loss and degradation (Meijaard and Sheil 2008). While we used expert derived assessments of the contribution of each land use zone to target achievement, there is evidently a need for further scientific evaluation of the ecological contribution of different land uses in production landscapes in East Kalimantan and elsewhere. Furthermore, an assumption in our analysis is that the contribution of each land use zone will remain stable through time but there is the potential for this contribution to vary spatially, as well as temporally. Such spatial and temporal dynamics are a natural, although non-trivial, extension to our integrated land use planning approach (Costello and Polasky 2004, Wilson et al. 2006).

While we focused on mammals in this analysis due to the availability of data, other taxonomic groups for which information exists on distribution, life history, and sensitivity could be similarly incorporated (Chung et al. 2000, Cleary 2004, Meijaard et al. 2005). The targets we used in this study were aimed to provide for the equitable protection of the mammalian fauna of East Kalimantan, although fail to account for the habitat connectivity, limits to dispersal, and interspecific interactions. In addition, for many species the detailed species-specific information required to develop the targets was not available and the parameters were often extrapolated from similar species. This was particularly the case for bats as home-range information is largely undocumented. While we found that our results were insensitive to the home range employed it is likely that the home ranges are underestimates due to a lack of information on the habitat use and behavior of many bat species. Bats represent approximately 40% of the mammal diversity of East Kalimantan and many bats are sensitive to forest disturbance, particularly insectivorous species that inhabit forest interiors (Lane et al. 2006, Struebig et al. 2010). It is important that initiatives to improve the ecological knowledge base of the mammalian fauna of East Kalimantan, and of Borneo generally, are supported. The SAMD database was an important contribution, and is indeed the most comprehensive database of species distribution in the study region, however the ongoing maintenance, improvement, and supplementation of such data is required (Meijaard and Sheil 2007*a*, Struebig et al. 2010).

Different land uses not only differ in their contribution to biodiversity conservation, but they also have different impacts on local economies and employment opportunities (Swallow et al. 2007). There may therefore be preferences for one land use over another in a given locality. We could account for this in our integrated land use planning approach by specifying targets for each land use or conservation strategy; for example aiming to achieve a certain percentage protected, a certain percentage in improved management, and a certain percentage in a converted state, such as under oil palm plantation (Watts et al. 2009). Such an extension would allow more specific socio-economic objectives to be incorporated, rather than just aiming to minimize the costs of biodiversity conservation. We could also specify desirable spatial relationships between zones, such as aiming for well-managed protected areas to be surrounded by reduced-impact logging operations.

While our analysis accounts for the potential impacts of habitat degradation on the conservation contribution of different land uses, a significant impact often associated with logging operations is the access that is provided for hunting (Robinson et al. 1999, Bennett and Robinson 2001, Marshall et al. 2006, Corlett 2007, Meijaard and Sheil 2008). Hunting affects those species important for food or trade, including bearded pigs, porcupine, pangolin (*Manis javanica*) and also some species of monkey and deer (Meijaard et al. 2006). The sustainable management of hunted wildlife is likely to be a component of reduced-impact logging activities, and the risk of wildlife extraction or potential accessibility of forest could be derived using information on distance from roads and trails, distance from rivers, distance from settlements and clearings, the perimeter to area ratio of each forest patch, human population density of the surrounding region, and other determinants of access such as slope and elevation (Harris et al. 2008, Drummond et al. 2009, Fuller et al. 2010).

We prioritized conservation investments in East Kalimantan to achieve prespecified and equitable conservation targets in a cost-efficient manner. We incorporated multiple land use zones and conservation strategies, the costs of each strategy, and the relative contribution of each land use zone to the conservation of biodiversity. The resultant conservation plans are based on several assumptions and while the best available data has been employed there are several aspects requiring improvement. The development of spatially heterogeneous cost data is a key area of further research, along with improved estimates of the contribution of each land use zone to conservation. As a consequence these results must be considered indicative only, as the analysis framework and the data employed will require substantial modification and stakeholder engagement before implementation. Our analysis does however reveal the potential for the costs of conservation to be overestimated if we assume that conservation targets can only be met through establishing new protected areas and that the unprotected matrix makes no contribution to the conservation goals. Our analysis indicates that it may be possible to achieve desired conservation outcomes at a cost that is more publically and politically digestible then if we restrict our strategies to the establishment of new protected areas. Notably, cost improvements were obtained without compromising targets for the persistence of species, particularly forest-obligates. Rather, improvements came from recognizing those species for which unprotected habitat have some conservation value. This is pertinent given the low likelihood that new protected areas will be established in the region (Moore et al. 2004). Our results emphasize the importance of political and industry support for sustainable forest management and for improved understanding of the contribution of production forests to biodiversity conservation. Our new framework for conservation planning provides information to support on-the-ground management decisions about not only where to invest, but how to invest in order to efficiently and effectively conserve biodiversity.

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APPENDIX

Life-history characteristics of 170 forest-dwelling mammal species occurring in East Kalimantan, Indonesia (*Ecological Archives* A020-062-A1).