Threat from deforestation to montane and lowland birds and mammals in insular South-east Asia

THOMAS M. BROOKS*†, STUART L. PIMM†, VALERIE KAPOS‡ and CORINNA RAVILIOUS‡

†*Department of Ecology and Evolutionary Biology, 569 Dabney Hall, University of Tennessee, Knoxville TN 37996–1610, USA; and ‡World Conservation Monitoring Center, 219 Huntingdon Road, Cambridge, UK*

Summary

1. A reduction in forest area should result in a reduction of its number of species and, moreover, do so in a characteristic way according to the familiar species-area relationship. Brooks, Pimm & Collar (1997) applied this formula to the losses in forest area in the Philippines and Indonesia. Independently derived totals of the number of endemic bird species that are threatened with extinction broadly agree with these predicted losses. In some cases, however, predicted losses overestimate or underestimate the actual numbers of threatened species.

2. Within an island, the proportionate deforestation to date might be most extensive where there are many endemic species, or where there are few. To test this possibility, we obtained recent forest cover data for the region. We separated lowland (< 1000 m a.s.l.) from montane (> 1000 m a.s.l.) forest cover by overlaying topographic maps. From these data, we predict separately the numbers of montane and lowland endemic bird species likely to become extinct as a result of deforestation. We then compared these totals with the numbers considered threatened in the latest *Red List*.

3. Our predictions based on deforestation closely match the numbers of threatened endemic birds in the lowlands, but underestimate them in montane regions.

4. Our predictions based on deforestation underestimate the number of threatened montane mammal species even more seriously.

5. Lowland faunas of insular South-east Asia are under extreme threat because of massive deforestation. The region's montane faunas appear seriously threatened even by low levels of deforestation.

Key-words: Indonesia, Philippines, Red Lists, tropical deforestation, species–area relationship.

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Introduction

Tropical deforestation clears approximately 10% of the original area per decade (Whitmore 1997), with about half that area already gone (Myers 1994). This causes a large and predictable loss of species (Pimm *et al.* 1995). On-the-ground surveys and satellite imagery document the proportion of forest that has been lost. Given this information, we can apply the insight from MacArthur & Wilson's (1967) classic theory. It stated that small habitat islands should contain fewer species than in larger blocks of continuous habitat, just as small oceanic islands have fewer species than larger ones. Thus, as habitat is reduced, species should be lost in a characteristic way. Only species endemic to the area are at risk of global extinction, however, although many other species could be lost locally. We consider only an area's endemic species and predict what fraction of them is likely to become extinct (Pimm & Askins 1995) as habitat shrinks.

We have applied this formula to the birds of eastern North America (Pimm & Askins 1995), the Atlantic forests of South America (Brooks & Balmford 1996) and insular South-east Asia (Brooks *et al.* 1997). For the first case, the major forest losses

were over a century ago and the predictions of extinctions match those observed. For the second and third cases, the predictions match the numbers of species considered threatened with 'a high risk of extinction in the wild in the medium-term future' in *Birds to Watch 2* (Collar, Crosby & Stattersfield 1994), the source on which the latest *Red Data Book* of globally threatened species is based (Baillie & Groombridge 1996).

The third—and most detailed—case indicated some important discrepancies between observed and predicted numbers (Brooks *et al.* 1997). In the Philippines and on Sumatra our predictions based on deforestation underestimated the number of threatened endemic species. In the Lesser Sundas, Java and Sulawesi our predictions overestimated the number of threatened endemic species. Several hypotheses could explain why this should be the case.

First, Collar *et al.* (1994) may overestimate the number of threatened species (in the Philippines and on Sumatra) or underestimate it (in the Lesser Sundas, Java and Sulawesi). As our knowledge of South-east Asian birds improves, we may recognize the 'responsible pessimism' of Collar *et al.* (1994) as being overly cautious. That is, if one does not know much about a species, it is likely to be rare. Collar *et al.* might then conclude that it is vulnerable. Better knowledge may show it not to be.

These cases may be balanced by three possibilities that lead to the underestimation of the true number of threatened species. One possibility is that new species will be rare ones—the common ones have all been found. Another is that taxonomic revisions typically split off local populations of more widely ranging species. In both cases, these additions to the list will probably be of threatened species (Cuarón 1993). The last possibility is that science may have failed to describe some endemics before humans drove them to extinction, as happened extensively in Polynesia (Pimm, Moulton & Justice 1994).

The second hypothesis is that our predictions underestimate the number of threatened species at high levels of deforestation, when at least two factors will cause a greater loss of species from the remaining small forest fragments than expected (Laurance *et al.* 1997). Small fragments will typically be more isolated from each other than large ones (With 1997). Moreover, small fragments have large ratios of forest edge to forest interior and forest edges sometimes are poor habitats for forest interior specialists (Murcia 1995).

Some patterns support this possibility. The extensively cleared Philippine forests have more threatened species than one expects and the still mostly forested Borneo has fewer. Other patterns, however, counter it. Our predictions underestimate threat on the still heavily forested Sumatra and overestimate

threat on the denuded islands of Java and the Lesser Sundas. In summary, the hypothesis cannot fully explain the discrepancies. Nonetheless, it begs our asking whether the details of the patterns of fragmentation might be useful in improving the formula's predictions.

Third, there is a pronounced moisture gradient within the region. The northern and western islands tend to be wetter and the southern and eastern islands tend to be drier (Whitmore 1984). The endemics of the dry monsoon forests of the lowlands of Lesser Sundas and, to a lesser extent, eastern Java and southern Sulawesi, may be able to adapt to the secondary growth and scrub that deforestation leaves behind.

Finally, deforestation is concentrated in the more accessible lowlands (Collins, Sayer & Whitmore 1991). The number of species threatened by deforestation should be larger for islands that have high levels of lowland endemism, like the Philippines (Dickinson, Kennedy & Parkes 1991), than in those where the endemics are predominantly montane, such as the Greater Sundas (Mackinnon & Phillipps 1993).

We present new data on the distribution of lowland and montane forest cover and endemism for both birds and mammals to explore these hypotheses.

Materials and methods

Our analysis requires three steps. First, we measure the distribution of remaining forest. Second, we predict the numbers of threatened species using the species-area relationship. Third, we compare these predictions to the independently assessed lists of threatened species.

MEASURING DEFORESTATION

Insular South-east Asia holds four archipelagos: the Philippines, the Greater and Lesser Sundas, and northern Wallacea (Fig. 1). The latter archipelago comprises the large island of Sulawesi and the smaller islands of the Moluccas. These, along with the Lesser Sundas, form the biogeographic province of Wallacea. We assume that historically all four archipelagos were forested (Collins *et al.* 1991), with predominantly moist forest in the north (where most deforestation is recent) and dry monsoon forest in the south (where much of the forest has been cleared for centuries). Brooks *et al.* (1997) gave a broad overview of the forest cover of the region.

We divide these four archipelagos based primarily on biogeography (e.g. Heaney 1986; ICBP 1992), combining, for example, Java with Bali, and Sulawesi with the Sula Islands. The bathymetry of the surrounding seas largely dictates this biogeogra-
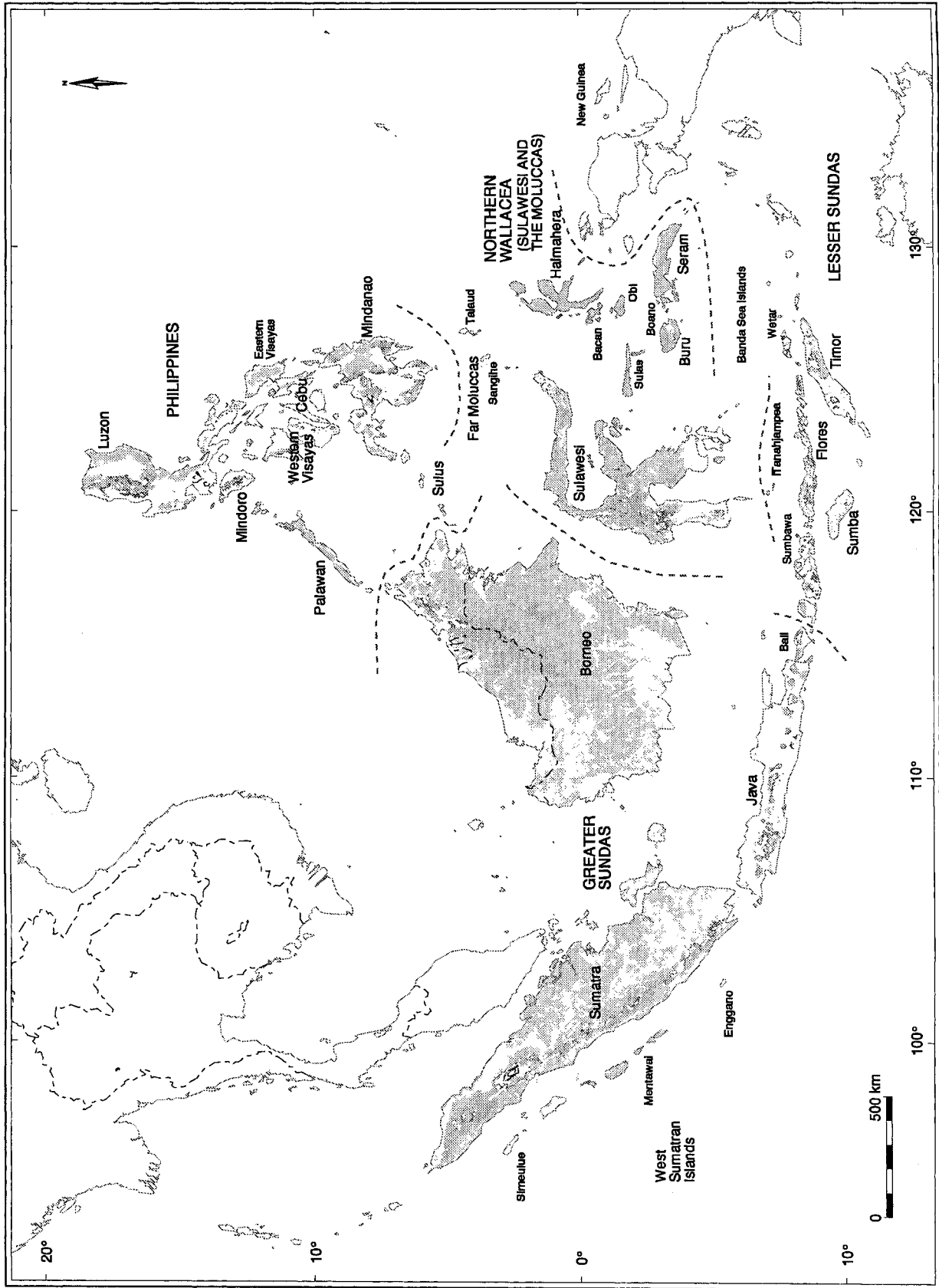
Fig. 1. Insular South-east Asia. The map shows lowland forest (light shading), montane forest (dark shading) and, in deforested (white) areas, the 1000 m contour. The four archipelagos are capitalized and demarcated by dashed lines. The island groups are named in normal type. Other islands referred to in the text are in small type.

phy. It determined which islands were connected during periods of lower sea level throughout the Pleistocene (Heaney 1991). We measure deforestation at the scale of these island groups (Fig. 1). Brooks *et al.* (1997) differed in not combining Simeulue, Mentawai and Enggano as the West Sumatran Islands (Holmes 1994) and including the tiny island of Tanahjampeah with the rest of the Lesser Sundas (Dutson 1995). Here, we also shorten terminology from Brooks *et al.* (1997), simplifying Sangihe and Talaud into the Far Moluccas (Lazell 1992) and the Central Visayas into simply Cebu (Dutson, Magsalay & Timmins 1993).

Increasingly comprehensive and accurate forest cover data for the tropics have become available as remote sensing and data handling technology have improved. In particular, the World Conservation Monitoring Centre and the Center for International Forestry Research have compiled spatial data in GIS form available on CD-ROM for the world's forests (Rhind & Iremonger 1996; Iremonger, Ravilious & Quinton 1997). For Indonesia, the most recent forest cover data (Rhind & Iremonger 1996) are updated versions of the RePPProT (1990) data. Collins *et al.* (1991) reproduced these and Brooks *et al.* (1997) used them. For the Philippines, the most recent data were provided to the World Conservation Monitoring Centre by the National Mapping & Resource Information Agency of the Philippines. Iremonger *et al.* (1997) reproduce them, updating the data published by SSC (1988), Collins *et al.* (1991) and Brooks *et al.* (1997). All of these data include both logged forest and plantation forest.

We analysed these data at the World Conservation Monitoring Centre, running the GIS Arc/Info version 7·0·4 (©Environmental Systems Research Institute, Inc. 1996). For each major island or group of small islands, we extracted values for the land area, forest cover, and hence percentage forest cover (Appendix 1). The small differences between these numbers and those presented in Brooks *et al.* (1997) are a combined result of improved accuracy in the data set and continuing deforestation in the region.

There is no clear-cut boundary between lowland and montane forest (Whitmore 1984). On steep slopes, forest that is montane can reach as low as 500 m a.s.l. Conversely, plateaus can hold forest that is lowland in character at altitudes well over 1000 m a.s.l. One consequence is that the transition from lowland to montane forest is at lower altitudes on small islands. These islands necessarily have their steepest slopes at a lower altitude. Nevertheless, the contour line of 1000 m broadly marks the transition between forest zones. We used this contour to define lowland and montane forest in our data set, recognizing that considerable variability exists.

The Digital Chart of the World (©Environmental Systems Research Institute, Inc. 1993), a global vector base map provided the contour data. For Borneo and Sulawesi, this source does not provide topographic data, and so for these islands we obtained that data from topographic maps. Four of the island groups are too low to have any montane forest under our definition—the Sulus, the Banda Sea Islands, the West Sumatran Islands, and the Far Moluccas. From the GIS database we extracted the land area and forest area and then calculated percentage forest cover for the lowlands and the mountains of the islands across the region (Appendix 1). Figure 1 shows the distribution of lowland and montane areas and forests.

PREDICTING NUMBERS OF EXTINCT AND THREATENED SPECIES USING THE SPECIES-AREA RELATIONSHIP

The species-area relationship, $S = cA^z$ (where S = number of species, A = area and c and z are constants), estimates the numbers of species found in different-sized areas (Preston 1962). Simple rearrangement of the relationship gives a prediction of the number of species that will eventually be lost when a particular habitat is reduced in size. Dividing $S_{surviving} = cA_{surviving}^z$ by $S_{original} = cA_{original}^z$ gives $S_{surviving}/S_{original} = (A_{surviving}/A_{original})^z$. Because $S_{extinct} = S_{original} - S_{surviving}$, we can derive $S_{extinct} = S_{original} - [S_{original}(A_{surviving}/A_{original})^z]$. Rosenzweig (1995) reviewed a wide range of empirical and theoretical work which suggests that for island situations the appropriate value for the exponent, z, is that originally derived by Preston (1962) of $\approx 0·25$. Appendix 1 provides values of $A_{surviving}$ and $A_{original}$ (and hence $A_{surviving}/A_{original}$) for the South-east Asian islands and island groups and for the lowland and montane portions of those islands. The data are expressed as percentages. Appendices 2 and 3 present the calculations of $S_{extinct}$ that we derive from them.

COUNTING SPECIES: ENDEMISM, ALTITUDINAL DISTRIBUTION AND CONSERVATION STATUS

We took our geographical data set for the birds of insular South-east Asia from Brooks *et al.* (1997). Stattersfield *et al.* (1998) published a similar data set for all birds with range sizes of $< 50\,000$ km². We cross-checked our data with this source for those species with sufficiently small ranges. Our taxonomy followed Sibley & Monroe (1990, 1993). We excluded the two additional Philippine birds given species status by Collar *et al.* (1994) and Baillie & Groombridge (1996). Our reason was that to include these while not including forms raised to species sta-

tus that are not threatened would introduce a small bias (Russell *et al*. 1998). For five species, the taxonomic treatment differs between Sibley & Monroe (1990) and Sibley & Monroe (1993): *Stachyris latistriata* (Gonzales & Kennedy 1990), *Caprimulgus manillensis* Walden 1875 and *C. celebensis* Ogilvie-Grant 1894 (Rozendaal 1990), *Collocalia esculenta* (Linnaeus) 1758 (Dickinson 1989) and *Otus alfredi* (Hartert) 1897 (Butchart *et al*. 1996). We also added a few species omitted in error from the totals in table 1 of Brooks *et al*. (1997).

Our geographical and habitat data come from the standard works for the region: Dickinson *et al*. (1991) for the Philippines, White & Bruce (1986), Andrew (1992) and Coates, Bishop & Gardner (1997) for Wallacea and Andrew (1992) and Mackinnon & Phillipps (1993) for the Greater Sundas. We include as northern Wallacea endemics five species [*Megapodius freycinet* Gaimard 1823, *M. wallacei* Gray 1860, *Eos squamata* (Boddaert) 1783, *Lichmera argentauris* (Finsch) 1870 and *Aplonis mysolensis* (Gray) 1862] which have outlying populations on tiny islands west of New Guinea (White & Bruce 1986). We excluded from our counts 16 species not in any way dependent on forested habitat.

Our data on altitudinal ranges come from these previously mentioned sources, supplemented by Jones, Linsley & Marsden (1995) for Sumba, Butchart et al. (1996) for Flores, Davidson, Stones & Lucking (1995) and Fraser & Henson (1996) for Sulawesi, Riley (1997) for the Far Moluccas, Lambert & Yong (1989) and Lambert (1994) for Halmahera, Marsden *et al*. (1997) for Buru, Bowler & Taylor (1989) and Moeliker & Heij (1996) for Seram, Poulsen (1995) for Luzon, and Evans, Dutson & Brooks (1993) for the Western Visayas, Cebu and Mindoro. We define montane endemics as those species only recorded above 500 m a.s.l. altitude, recognizing that species nearly always found above 1000 m a.s.l. will sometimes stray to lower elevations. It is possible that a few of our montane species are only montane because all of their habitat has been lost from the lowlands, although this is impossible to test. This leaves a broad category of lowland endemics including both species only found in lowland forest and a few species (mainly supracanopy birds such as raptors and swifts) that are found at all altitudes but for which the much larger proportion of the range is lowland (e.g. McGregor 1920).

As in Brooks *et al*. (1997), we took data on conservation status from the latest summary *Red Data Book*, Collar *et al*. (1994) and Baillie & Groombridge (1996). Following the rediscovery of *Dicaeum quadricolor* (Tweeddale) 1877 (Rabor 1959; Dutson *et al*. 1993) and *Eutrichomyias rowleyi* (Meyer) 1878 (Whitten *et al*. 1987; Riley 1997) no

forest species remain on the list of species proven extinct in the region. Later, we discuss the possibility that a number of species could have been lost without our knowledge (Balmford 1996).

We did not include in the threatened totals any species for which Collar *et al*. (1994) do not list habitat destruction as a threat. Thus we exclude from these totals the 11 species in the region listed under criterion D ('a very small population and/or a very small range'), as these are not threatened by current deforestation. We also excluded poorly known 'Data Deficient' species and those listed as 'Near Threatened' or 'Conservation Dependent'.

We should also exclude any species threatened not by deforestation but by direct human exploitation (under criteria A1c and/or A2c), but no bird species in the region are listed solely under these criteria (Collar *et al*. 1994). Earlier, we (Brooks *et al*. 1997) did exclude five species of Wallacean parrots [*Lorius garrulus* (Linnaeus) 1758 and *Cacatua alba* (Müller) 1776 from Halmahera, *L. domicella* (Linnaeus) 1758 and *C. moluccensis* (Gmelin) 1788 from Seram, and *C. sulphurea* (Gmelin) 1788 from the Lesser Sundas and Sulawesi] that are primarily threatened by the cage-bird trade (Smiet 1985). In this analysis, we include these species, because all five are also under threat from habitat destruction (Collar *et al*. 1994). We did this for two reasons. The first was for consistency, because a number of other birds are threatened by direct exploitation as well as habitat loss (Collar *et al*. 1994). The second is because, realistically, threat from direct exploitation will increase as habitat loss increases (Diamond 1984).

A number of future changes may affect the number of species likely to become extinct in the region. The discovery of new species or taxonomic reassessment of existing forms may increase the number of species considered threatened (Cuarón 1993). Only two definite new species—*Aethopyga linaraborae* (Kennedy, Gonzales & Miranda 1997) and *Gymnocrex talautensis* (Lambert 1998)—have been described in the region since the publication of Collar *et al*. (1994). The status of another new (nonforest) species, *Lonchura pallidiventer* (Restall 1996) is unclear, because it is known only from trade specimens, probably derived from Borneo. Three further new species from the Philippines—a woodcock *Scolopax* sp. (Harrap & Fisher 1994), a bleeding-heart *Gallicolumba* sp. (Klop, Curio & de Soye 1998) and a shortwing *Brachypteryx* sp. (Morris 1996)—have yet to be formally described. Nevertheless, the number of new species will probably be low.

In contrast, the extent of taxonomic 'splitting' and 'lumping' is likely to be relatively high. It will be reflected in, for example, the forthcoming *Threatened Birds of Asia* (N.J. Collar, personal com-

munication). Scanning an extensive but not exclusive list of recent references (Andrew 1992; Brooks *et al.* 1992; Dutson 1993; Evans *et al.* 1993; Mackinnon & Phillipps 1993; Madge & Burn 1993; van Balen 1993; Rozendaal 1994; Collar & Long 1995; Jones, Dekker & Roselaar 1995; Mees 1995; Tobias 1995; Lambert & Woodcock 1996; Coates *et al.* 1997; Stattersfield *et al.* 1998) in which taxonomy differs from Sibley & Monroe (1990, 1993) provides us with maxima of 18 species to be gained through 'splitting' and 22 species lost through 'lumping'. Thus, the net total of 'splits' and 'lumps' will make little difference to the total number of species.

Continuing deforestation across the region (Whitmore 1997) will certainly cause many more species to become threatened. In contrast, the very act of listing the region's species as threatened will hopefully act as a conservation catalyst (Collar 1996). While we recognize that in combination these factors will probably lengthen the list of threatened species, we conservatively restrict our analysis to species listed as threatened by Collar *et al.* (1994) alone. Appendix 2 summarizes the bird data.

We extend our analyses to mammals. There must be gaps in the mammal data, for even the distribution of North American mammals is incompletely known (Grayson & Livingston 1993). Heaney (1997) reports that at least 13 new species are currently being described from the Philippines alone. However, the region's mammal faunas are in broad agreement with general biogeographic patterns (Heaney 1986), suggesting that they are well enough known for us to make coarse predictions of the number of endemics that will become extinct following deforestation.

We compile a database of the region's endemic mammals. Our source was the latest taxonomy and distribution of the world's mammals, Wilson & Reeder (1993). All the endemic species for which Wilson & Reeder (1993) give habitat information are forest species. Furthermore, Heaney *et al.* (1989) found that forest mammals in the central Philippines tended to be endemic to particular islands, while species of deforested areas tended to have wide global ranges. Consequently, we assume that forest is the habitat for all endemic mammals of insular South-east Asia.

There are fewer data for altitudinal ranges for mammals than for birds. We again take this information from Wilson & Reeder (1993), which on occasion presents explicit ranges. More often we have to rely on qualitative information given by Wilson & Reeder (1993) or even, for the least-known species, simply whether or not the type locality is listed as a mountain. We use Musser (1987) for Sulawesi (who gives explicit altitudinal ranges

for nonvolant mammals), and Payne, Francis & Phillipps (1985) for all Bornean endemics.

We take our list of threatened and extinct species from Baillie & Groombridge (1996). Six insular South-east Asian endemic mammals are listed as extinct, although numerous other species may have been lost (e.g. Terborgh 1974). Of the known extinctions, two are recent losses of fruit bats from the Western Visayas (Heaney & Heideman 1987). In contrast, three rodents from Flores (Musser 1981) and one from Timor (Glover 1986) are known only from fossil deposits 3550 years old. We include these species because a small possibility remains that they survive to the present (Wilson & Reeder 1993).

We exclude from consideration 17 taxa that Baillie & Groombridge (1996) deem to be species, but Wilson & Reeder (1993) do not. Twelve of these are 'lumped' by the latter, one was described too recently (Gonzales & Kennedy 1996) to be included, and four ('*Otomops johnstonei*', '*Apomys gracilostris*', '*Hipposideros madurae*'' and '*H. sorensoni*') we have not been able to trace. We do not count 21 species as threatened by deforestation. Of these, 19 are endemic to one of the archipelagos, the other two are widespread within the region. These 21 are listed as under pressure from direct exploitation only (*Red List* criteria A1c and/or A2c). We also exclude a further 13 species listed as threatened by their naturally tiny ranges and/or populations (criteria D1 and/or D2).

As with birds, we recognize that Baillie & Groombridge (1996) will almost certainly underestimate likely species extinction as a result of the effect of taxonomic revision (e.g. Heaney 1997) and accelerating deforestation (e.g. Whitmore 1997). Nevertheless, we once again take the *Red List* (Baillie & Groombridge 1996) as our conservative, empirical estimate of which insular South-east Asian endemic mammals are likely to become extinct in the medium-term future. Appendix 3 summarizes the mammal data.

Results

BIRDS

Table 1 compares the observed numbers of threatened and nonthreatened endemics to those numbers of endemics predicted to be threatened and not to be threatened on the basis of the extent of deforestation. As a specific example, there are 182 species of birds endemic to the Philippines. Of these, 71 are threatened with extinction, while 111 are not. Predicted numbers arise as follows. Luzon has 25% of its forests remaining (Appendix 1). There are 25 species endemic to the island (Appendix 2), and from the extent of deforestation, the species-area formula predicts that 7·3 should be threatened. (Predicted values need not be integer values.)

Table 1. Endemic birds of insular South-east Asian archipelagos. See text for data sources. We compare the numbers of species threatened (Collar *et al.* 1994) and not threatened that are endemic to each archipelago with the numbers of endemic species predicted by deforestation to become extinct and to survive. In each case our null hypothesis is that deforestation predicts the number of threatened species (Brooks *et al.* 1997). For each archipelago we give a χ^2-value and its significance level for this comparison. All tests have 1 d.f. In cases where an expected value is less than 5, the sampling distribution of χ^2 no longer approximates the chi-squared distribution, and so we apply Yates' correction (Spiegel 1994). We indicate in parentheses the effect of excluding from the observed counts of threatened species the Wallacean parrots which are threatened by trapping as well as habitat destruction

Archipelago	Endemics	Threatened		Non-threatened		χ^2	P
		Observed	Predicted	Observed	Predicted		
All species							
Philippines	182	71	55·5	111	126·5	6·2	0·02
Lesser Sundas	86	12	25·0	74	61·0	9·5	< 0·01
Greater Sundas	111	17	21·2	94	89·8	1·0	0·30
North Wallacea	166	21(17)	17·3	145(149)	148·7	0·9(< 0·1)	0·30(0·85)
Montane species							
Philippines	44	23	4·6	21	39·4	79·4	< 0·01
Lesser Sundas	12	4	2·6	8	9·4	0·7	0·35
Greater Sundas	80	8	5·7	72	74·3	0·7	0·35
North Wallacea	47	3	1·4	44	45·6	1·1	0·30
Lowland species							
Philippines	138	48	46·5	90	91·5	0·1	0·75
Lesser Sundas	74	8	21·2	66	52·8	11·6	< 0·01
Greater Sundas	31	9	12·6	22	18·4	1·7	0·20
North Wallacea	119	18(14)	14·2	101(105)	104·8	1·2(< 0·1)	0·25(0·85)

Comparable predicted numbers of threatened species for Mindoro, the Western Visayas, Cebu, Mindanao, the Sulus and Palawan are 2·6, 4·4, 3·0, 9·8, 1·7 and 2·7, respectively, for a total of 31·5 species. There are 82 species found across the Philippines but not outside the archipelago (Appendix 2). Averaged over the archipelago, 25% of the forest remains (Appendix 1), so of these 82, we predict that 24·0 should be threatened. Combined, 55·5 species should be threatened, and thus $182 - 55\cdot5 = 126\cdot5$ should not be threatened.

The null hypothesis is that our predictions based on deforestation match known threat, and thus that observed and predicted numbers do not differ more than expected by chance. The χ^2 for the comparison, 71 observed vs. 55·5 predicted and 111 observed and 126·5 predicted, is 6·2. The probability of this happening were the null hypothesis true is $P = 0\cdot02$ and so we reject that hypothesis. Our predictions do not accurately match the numbers of threatened species.

The first four lines of Table 1 recap Brooks *et al.* (1997). The formula satisfactorily predicts the observed numbers of threatened species on the Greater Sunda and Northern Wallacea. It significantly underestimates them in the Philippines, and overestimates them in the Lesser Sundas.

The second and third analyses are for montane and lowland forests, respectively. An interesting pattern emerges. The species-area formula underestimates the threat to montane species in the Philippines and overestimates the threat to lowland species in the Lesser Sundas. The remaining six comparisons are not significantly different from what deforestation predicts. Non-significant results are in the majority. This means that our formula satisfactorily predicts the number of threatened species. There are two significant results, however, and it is these refutations of our model that we seek to understand.

Comparisons of the island-by-island predictions (Appendix 2), show that our species-area formula consistently underestimates the threat to montane species. In the Philippines, the observed numbers of threatened species exceed those predicted on four of the five islands that hold montane endemics. The exception is Palawan, which has only two montane endemics and 96% of its montane forest remaining. Neither species is threatened, nor would we expect either to be, given that so much of the forest remains. On all three of the Lesser Sundas island groups that have montane endemics, the observed numbers of threatened species exceed those predicted. In the Greater Sundas, Sumatra has six threatened montane species; our predictions suggest that only one should be. For Java, Bali and Borneo combined, our formula predicts 3·3 threatened species, whereas there are only two. For Northern Wallacea, three islands have one threatened species each; we predict that only one of these islands should have a threatened species.

For the lowlands, comparisons of the island-by-island predictions (Appendix 2), show no consistent deviation from what the species-area formula predicts, with the aforementioned exception of the

Lesser Sundas. There are 20 independent contrasts of predicted and observed numbers of threatened species. Observed values are smaller than expected values for 7 of these, larger for 12, and there is one tie. On the Lesser Sundas, however, the overall pattern is for the predictions to overestimate threat consistently. This applies to each of the four island groups, and to species found throughout the Lesser Sundas, but nowhere else.

We separate the four lowland North Wallacean parrot species (*C. sulphurea* occurs in the Lesser Sundas as well as on Sulawesi) that we did not count as threatened in Brooks *et al.* (1997) within the totals of threatened species (Table 1). Our inclusion of these species further increases the degree to which our observed values match the predictions in North Wallacea.

MAMMALS

Table 2 repeats the analyses for mammals. Once again, the deviations from the expectations from deforestation separate according to whether the species are montane or lowland. The observed numbers of threatened lowland species are satisfactorily predicted by the extent of the deforestation both within each archipelago (Table 2) and across the 20 independent island-by-island comparisons (Appendix 3). There are slightly more threatened mammals in the lowlands of the Lesser Sundas than we predict, rather than significantly fewer than predicted for birds.

There are only two montane endemics in the Lesser Sundas, so we cannot draw any conclusions. In the other three archipelagos, the predicted numbers of threatened species are significantly fewer than those observed. In the 16 independent contrasts of predicted and observed numbers (Appendix 3), observed numbers exceed predicted numbers 10 times, and there are 4 ties. All the ties are cases where the prediction is that no species should be threatened and none are.

We indicate in Table 2 the effect of including those mammals listed by Baillie & Groombridge (1996) as threatened by direct exploitation only. In nearly every case, this would increase the degree by which our number of threatened species exceed our predictions. For the few montane cases, their inclusion further increases the statistical significance of the already significant tests. For the lowlands of three archipelagos, the inferences change. With the inclusion of these species, deforestation significantly underestimates threat.

Discussion

Across insular South-east Asia, for birds and mammals, we satisfactorily predict the numbers of threatened species, based on the extent of deforestation, with three key exceptions. In increasing order of importance:

1. If we include in our counts of threatened species those 21 mammal species which are threatened solely by direct human exploitation (Baillie & Groombridge 1996), then our predictions underestimate threat in nearly all lowland regions.

2. We consistently overestimate the degree of threat to birds in lowland habitats across the Lesser Sundas.

3. The predicted numbers of threatened species of birds and mammals derived from estimates of deforestation consistently underestimate the observed

Table 2. Endemic mammals of insular South-east Asian archipelagos. See text for data sources and Table 1 legend for details of the structure of the table and mechanics of the comparisons. We indicate in parentheses the effect of including in the observed counts of threatened species the 21 species which are threatened by hunting alone

Archipelago	Endemics	Threatened		Non-threatened		χ^2	P
		Observed	Predicted	Observed	Predicted		
All species							
Philippines	100	39(47)	28·3	61(53)	71·7	5·7(17·2)	0·02(< 0·01)
Lesser Sundas	20	10(11)	7·2	10(9)	12·8	1·7(3·1)	0·20(0·07)
Greater Sundas	114	32(39)	18·7	82(75)	95·3	11·4(26·4)	< 0·01
North Wallacea	93	25(28)	10·3	68(65)	82·7	23·8(34·2)	< 0·01
Montane species							
Philippines	39	16(18)	4·4	23(21)	34·6	32·7(34·6)	< 0·01
Lesser Sundas	2	0	0·5	2	1·5	2·0	0·15
Greater Sundas	50	17	3·0	33	47·0	64·6	< 0·01
North Wallacea	37	19(20)	1·2	18(17)	35·8	262·4(289·5)	< 0·01
Lowland species							
Philippines	61	23(29)	18·5	38(32)	42·5	1·6(8·6)	0·20(< 0·01)
Lesser Sundas	18	10(11)	6·8	8(7)	11·2	2·5(4·2)	0·10(0·05)
Greater Sundas	64	15(22)	11·1	49(42)	52·9	1·6(12·9)	0·20(< 0·01)
North Wallacea	56	6(8)	7·4	50(48)	48·6	0·3(0.1)	0·60(0·75)

numbers in montane forests. What could explain these exceptions?

GENERAL PROBLEMS OF BIAS

One worry is that the *Red List* may not have been compiled independently of the extent of deforestation. As a hypothetical example, suppose that Collar *et al.* (1994) looked at the island of Cebu and, from their knowledge that only a few hectares of the island's forest remain, concluded (correctly) that all its endemic species would be on the verge of extinction. Such a process would guarantee a match between observed and predicted numbers of threatened species, when all the island's species are threatened. As we discussed in Brooks *et al.* (1997), the decisions of Collar *et al.* (1994) and Baillie & Groombridge (1996) to list species were made based on case-by-case review (with habitat loss within the species' range only one of the factors considered). In any case, this process would not so readily obtain a match when not all the island's species should be threatened. How many species should they choose—and which ones? Nor does the hypothetical example explain the results where observed and predicted numbers diverge so consistently.

Another possibility is that observed numbers of threatened species might be higher than predicted because the species may be threatened by factors other than deforestation. These factors will tend to be correlated with habitat loss (Diamond 1984). It may be easier to hunt in forest fragments or from forest edges, for example. We try to control for these possibilities in three ways.

First, we excluded all species listed as threatened solely as a result of their being hunted, trapped or otherwise exploited. We discuss the consequences of including these below. We included the many species that are listed because of deforestation as well as direct exploitation (e.g. O'Brien & Kinnaird 1996). Our results would not have changed significantly had we excluded the five lowland Wallacean parrots that are threatened by deforestation as well as by trapping (Table 1). Second, we excluded all species threatened because of their tiny ranges alone, regardless of the extent of deforestation. Third, we checked that no species were listed as threatened based on projected future threat only (criterion A2): none are, although it is not impossible that future threat could also be included in the B criterion.

UNDERESTIMATES OF THREAT TO LOWLAND MAMMALS

Baillie & Groombridge (1996) list 21 species of mammals as threatened by direct exploitation alone:

seven Philippine endemic bats [*Acerodon leucotis* (Sanborn) 1950, *Haplonycteris fischeri* Lawrence 1939, *Nyctimene rabori* Heaney & Peterson 1984, *Otopteropus cartilagonodus* Kock 1969, *Pteropus leucopterus* Temminck 1853, *P. pumilus* Miller 1911 and *Rhinolophus subrufus* K. Andersen 1905] and one flying lemur [*Cyanocephalus volans* (Linnaeus) 1758]; the bat *Dobsonia peroni* (E. Geoffroy) 1810 from the Lesser Sundas; four bats (*Nycteris javanica* E. Geoffroy 1813, *Pipistrellus cuprosus* Hill & Francis 1984, *Mormopterus doriae* K. Andersen 1907 and *Otomops formosus* Chasen 1939) and three primates [*Nasalis larvatus* (Wurmb) 1787, *Presbytis potenziani* (Bonaparte) 1856 and *Hylobates klossii* (Miller) 1903] from the Greater Sundas; the bat *Hipposideros inexpectatus* Laurie & Hill 1954 and the palm-civet *Macrogalidia musschenbroekii* Schwarz 1910 from Sulawesi; the bat *Acerodon humilis* K. Andersen 1909 from the Far Moluccas; and two endemics widespread within insular South-east Asia, the primate *Trachypithecus auratus* (E. Geoffroy) 1812 and the rodent *Haeromys pusillus* (Thomas 1893). That two-thirds of these species are bats is not surprising. Bats are heavily hunted throughout the region (Heaney & Heideman 1987). But why should including these heavily hunted species cause deforestation to underestimate threat in the lowlands but not in the montane regions? The explanation is simply that people live in the flat lowland regions. Lowland mammals are threatened beyond what we expect as a result of deforestation simply because their habitat is accessible to their human predators.

OVERESTIMATES OF THREAT IN LOWLAND MONSOON FOREST

The lowland birds of the monsoon forests of Java and the Lesser Sundas are less threatened than the extent of deforestation would predict. These islands, because much of their forest has been cleared for centuries, may have lost lowland endemics before they were known to science (van Balen 1994).

One of these missing endemics could have been *Argusianus bipunctatus* (Wood) 1871, known only from a portion of a male primary feather described in 1871 (Davison 1983; Sibley & Monroe 1990), although the validity of this taxon is in doubt (Parkes 1992). Delacour (1951) noticed that Java is the most obvious gap in the Sundaic range of the congeneric *A. argus* (Linnaeus) 1766, and suggested that *A. bipunctatus* had replaced the species there. Davison (1983) argued that because Javan ornithology dates back 'much earlier than the discovery date of *A. bipunctatus*' the species was more probably from Tioman, off peninsular Malaysia. However, there is no reason that the feather could not have been obtained on Java well before 1871. Another missing endemic could have been *Gallirallus sharpei*

(Büttikofer) 1895 known from a single specimen purchased in Amsterdam in 1865, and which Olson (1986) argued must have derived from the Sundaic region. By comparing the lowland avifaunas of Java with Borneo and Sumatra, van Balen (1994) further speculates that trogons, malkohas and frogmouths have also been lost. Only archaeological exploration will be able to provide further evidence for this 'missing species' hypothesis (Pimm *et al.* 1994).

Alternatively, our results could support a second hypothesis that the birds endemic to dry monsoon forest are more tolerant of deforestation than are moist forest species. This remains to be tested elsewhere and it does have broader relevance; for example, the New World dry forests are the 'most endangered tropical ecosystem' (Janzen 1988). Interestingly, only 17% of the region's threatened birds are dry forest species, compared to the 57% that are moist forest species (Collar, Wege & Long 1997). The proportions of total dry and total moist forest species considered threatened are not known, but the data do suggest that dry forest species may be under proportionately less threat. A similar example comes from the largely deciduous forests of the Western Ghats of India. Despite the fact that these 'have been much degraded by human activities', none of their 19 endemic bird species are considered threatened (Gaston & Zacharias 1996). Their birds are 'largely opportunistic habitat users' (Daniels 1996), able to adapt to, or at least forage in, coffee plantations (Shahabuddin 1997). These patterns should not be interpreted as suggesting that dry forest species are unharmed by deforestation.

These two hypotheses are not necessarily exclusive. Monsoon forests are more easily settled by people than are rainforests, and so the drier southern islands of the region have been inhabited for a longer time than the rainforest islands (Collins *et al.* 1991). Ancient deforestation in the lowlands of Java and the Lesser Sundas could have provided an 'extinction filter' (Balmford 1996), driving the most vulnerable species to extinction while the survivors adapted to the remaining degraded habitats.

For mammals, deforestation does not overestimate threat in the Lesser Sundas. This may be a result of inclusion in the *Red List* of the Lesser Sundas' four (probably) long-extinct species (Musser 1981; Glover 1986). This would be consistent with the 'missing species' hypothesis. At least three more extinct murids are known from Timor but await formal description (Glover 1986). Alternatively, we might expect mammals, being poor dispersers (Brown 1971), to be less tolerant than birds of the fragmentation of any kind of forest. If this is the case, then we should not be surprised to find that lowland deforestation overall predicts threat to the region's mammals very well.

UNDERESTIMATES OF THREAT IN MONTANE FOREST

Why are more montane species threatened than we expect from the loss of habitat? There are several hypotheses. First, what if the underestimate of the level of threat based on deforestation is really a consistent overestimate of the level of threat by the *Red List*? Perhaps montane endemics, with naturally tiny ranges and populations, are perceived to be more threatened than they actually are. In our analysis, we assumed that the listing process rigidly followed the IUCN criteria for threatened status (Baillie & Groombridge 1996). All species threatened only by naturally tiny ranges or populations should have been listed under criterion D—which we exclude. If such species have been perceived as rarer than they are—perhaps because of the difficulties of carrying out fieldwork in montane forest—the *Red List* may overestimate threat to montane endemics. Only further detailed fieldwork will answer this possibility.

Second, our species-area formula based on deforestation may underestimate the threats in montane forest because fragmentation can threaten species over and above the loss of area alone (Laurance *et al.* 1997). As a simple product of their rugged topography, might remaining montane forests have proportionately more forest edge than those surviving lowland forests? This hypothesis is straightforward to test if we consider that as levels of fragmentation increase, the ratio of edge: area will increase as well (Krummel *et al.* 1987). For the Philippines forests, Dawning, Iverson & Brown (1993) found that forest patches with a high edge to area ratio in 1934 tended to be small and likely to be deforested subsequently.

From the GIS data, we calculated the length of forest–nonforest edge (i.e. excluding the length of the forest–sea and lowland forest–montane forest edges) for montane and lowland habitats on all islands (Appendix 1). The edge-to-area ratio is scale dependent, so we calculated the value of edge divided by square root of area. We then compared these values using a two-tailed Wilcoxon rank test. The edge to square root of area was significantly greater in lowland than in montane forest across all of the islands ($t = 3.92$, 19 d.f., $P < 0.01$). The results reject the hypothesis that montane forest is more fragmented than lowland forest.

The third and fourth hypotheses suggest that there are systematic differences between the ranges of montane and lowland endemic species. Hypothesis three is that montane endemics, unlike lowland endemics, might have generally complementary ranges; for example, each mountain range might have its unique species. The larger the area sampled, the more mountain ranges would be included, and so the more species. Species numbers

would increase in direct proportion to the area and so the species to area relationship would have a slope of unity. If this were the case, the destruction of forests would reduce the number of species in direct proportion to the area lost. Lose half the forest and lose 50% of the species—a considerably greater loss than the 15% loss predicted for a species-to-area relationship with an exponent of 0·25.

We can test hypothesis three in two ways: directly, by looking at whether the distributions of montane endemics are indeed complementary; and indirectly, by examining the slope of the species-to-area relationships.

Within the mountains of Mindoro, Palawan, Halmahera, Buru, Seram, Sumba and Timor the distributions overlap almost completely. On Luzon, Mindanao, Java and Flores, the distributions are nested within those of the most widely occurring species. No distributions are complementary to each other. On Sumatra, with 14 montane endemics, one species pair is complementary between the North and South Barisan range, *Lophura hoogerwerfi* (Chasen) 1939 and *L. inornata* (Salvadori) 1879. These forms may actually be a single species (Mackinnon & Phillipps 1993). On Borneo, with 28 montane endemics, only one species, *Oriolus hosii* Sharpe 1892, does not occur on the largest mountain, Mt Kinabalu, being replaced there (and elsewhere in the Greater Sundas) by the widespread *O. cruentus* (Wagler) 1827 (Mackinnon & Phillipps 1993). On Sulawesi, with 29 montane endemics, there is a single complementary species pair, *Cyornis sanfordi* Stresemann 1931 (endemic to the Minahassa Peninsula) and *C. hoevelli* (Meyer) 1903 (elsewhere on the island) and one species endemic to the isolated Lompobattang massif, *Ficedula bonthaina* (Hartert) 1896 (Fraser & Henson 1996). The distributions of montane endemics are perfectly complementary in only one case, the Western Visayas, where the three species have nonoverlapping ranges (Dickinson *et al.* 1991): *Ptilinopus arcanus* Ripley & Rabor 1955 on Mt Canlaon, northern Negros; *Stachyris latistriata* on Mt Baloy, Panay; and *S. nigrorum* Rand & Rabor 1952 on Mt Talinis, southern Negros.

In summary, very few of the single-island montane endemic birds of the region have complementary distributions. These observations reject the possibility that a high level of complementary montane endemism accounts for the disproportionately high threat that we observe to montane endemics.

Figure 2 plots the numbers of montane and lowland endemics (Tables 1 and 2) against their potential ranges (Appendix 1). These are endemics-area relationships (Harte & Kinzig 1997). Were the slopes of the montane species steeper than for the lowlands, this would both suggest greater complementarity in montane ranges and a greater suscept-
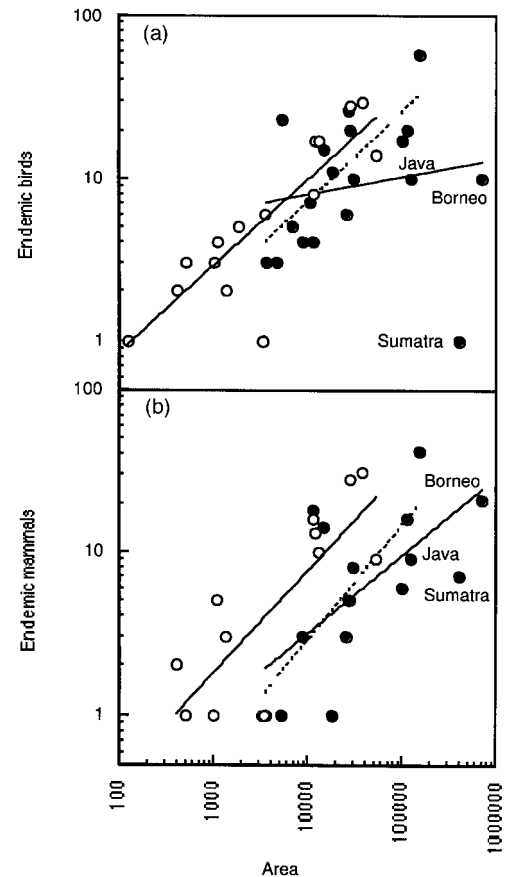
Fig. 2. Endemics–area relationships. These are plots (on log-log scales) of the numbers of (a) endemic birds and (b) mammals in both montane (○) and lowland (●) regions of South-east Asian islands. We fit power functions to these plots, excluding from the lowland data the landbridge islands of Sumatra, Java and Borneo, which have proportionately less lowland endemics than oceanic islands. We find that these plots are no steeper for montane species (exponents of 0·54 for birds and 0·63 for mammals) than for lowland species (exponents of 0·55 for birds and 0·70 for mammals). This indirectly illustrates that the region's montane faunas are no more geographically nested than its lowland faunas.

ibility to deforestation. The lowlands of Sumatra, Java and Borneo have far fewer endemics than one would expect from their size. This is not surprising: these islands had Pleistocene connections to mainland South-east Asia (Heaney 1986). Excluding them, the log-log fits of species to area are nearly identical for montane and lowland birds and similar for montane and lowland mammals.

In summary, the endemic area relationships also reject a difference in the patterns of the ranges of montane and lowland species that would explain the greater levels of threat suffered by the former.

The fourth hypothesis is that species with small ranges may be disproportionately threatened by a given proportionate forest loss. This could be a per-

ception, rather than reality—the consequence of classifying any species with a very small range as being threatened, even in the absence of direct evidence. Such perceptions may have a high probability of becoming reality, of course, because habitat destruction can quickly drive such species to extinction.

The disproportionate threat could also be a real effect for one of several reasons. Other things being equal, a temporary reduction in numbers, say 50%, is no threat to a population numbering in the millions, but it would be a matter of concern to a population numbering in the hundreds, and would be fatal to a population of two individuals.

Other things are often not equal, making life even harder for species with small ranges. Typically such species are less dense within their ranges than are more widespread species (Brown 1984). Less abundant species are more vulnerable than common species (Pimm 1991). The argument against this possibility is that correlation of range size and density is, at best, one with much variation. Across this region, many montane species are extremely common within their tiny ranges, maybe as a result of density compensation (MacArthur, Diamond & Karr 1972) in their depauperate communities (Terborgh 1977). A good example is *Stachyris nigrorum*, which we found to be the second most common bird on Mt Talinis (in South Negros in the Western Visayas), the single mountain from which it is known (Brooks *et al.* 1992). Only fieldwork to determine accurate population densities for the insular South-east Asian endemic species will resolve this problem.

The critical questions ask: Are species at greater risk than expected because they have small ranges? If so, are montane species at greater risk because a greater proportion of them have smaller ranges?

The numbers are too small to break down these results by archipelago. Across the four archipelagos, there are 183 montane endemic birds (Appendix 2), of which 141 occur only on one island, and 42 occur on more than one island within each archipelago. Of the more widespread 42 species, only four are threatened and deforestation predicts this number almost exactly (3·7). It is montane species found only on single islands that are disproportionately threatened: 34 are threatened, compared to the prediction of only 10·4. For mammals (Appendix 3), there are only seven widespread montane endemics, one is threatened, which matches the prediction. Again, the threatened species are endemics found on single islands.

These numbers are too few to draw strong conclusions. Nonetheless, they suggest that it is not the fact of being montane that makes a species unusually threatened. Being montane usually means being restricted to one island, and, by our definition,

the montane forests of that island. Such species have typically the smallest ranges of those we consider. We do not have estimates of the ranges of all the species, so we cannot make the obvious comparison to those lowland species that have very small ranges.

This systematic failure of the predictions of threat when applied to species with the smallest range sizes matches our earlier conclusion (Brooks *et al.* 1997). We found then that endemics restricted to single islands were more threatened, compared to predictions, than species found throughout an archipelago. These, in turn, are more threatened, compared to predictions, than species found throughout the region.

CONCLUSIONS

The biodiversity of Indonesia and the Philippines is under great threat. Montane species are disproportionately threatened, because, we assert, they have the smallest ranges. This finding has precedents. Renjifo *et al.* (1997) recently highlighted the disproportionate threat faced by montane avifaunas in the northern Neotropics. Within insular South-east Asia, the discovery of *Aethopyga linaraborae* by Kennedy, Gonzales & Miranda (1997) has attracted attention to the highland birds of Mindanao. Crucially, the lowlands of insular South-east Asia hold by far the greater absolute numbers of threatened species. These lowlands should therefore remain key elements of conservation strategy, supplemented by montane areas.

Our analysis indicates that threat to insular South-east Asian mammals, especially the montane endemics, is underestimated by the extent of deforestation. This is well-documented (Oliver 1994; Heaney 1997). It is also not surprising. We would expect poor dispersers like mammals to be particularly susceptible to habitat loss (Brown 1971). Furthermore, while 11% of the world's birds are threatened, 25% of mammals are threatened (Baillie & Groombridge 1996). The pattern results from there being so many mammals with small, montane distributions. This has implications for conservation strategy. Hague *et al.* (1986) showed that distribution patterns across the Philippines are similar across higher taxa and hence indicated that conservation planning could be based on any one taxon (but see van Jaarsveld *et al.* 1998). Our results suggest that it is important to compare patterns of threat as well as patterns of distribution to choose a given higher taxon (e.g. birds or mammals) as a baseline for conservation strategy.

Finally, estimates of the total size of the 'sixth extinction' usually make arguments based on projections of tropical forest loss, the known fraction of species found in tropical forests, and the species to

area relationship. One such argument runs 'if we protect 5% of the forests in national parks, then we will likely save 50% of the 80% of all species, the fraction that is found within those forests.' Our results show that this argument is flawed. Saving 5% of tropical forests will not save as many as 50% of the original forest species if those parks are small ones.

Acknowledgements

References

Andrew, P. (1992) *The Birds of Indonesia. A Checklist (Peters' Sequence)*. Kukila Checklist no. 1. Indonesian Ornithological Society, Jakarta.

Baillie, J. & Groombridge, B. (1996) *1996 IUCN Red List of Threatened Animals*. The IUCN Species Survival Commission, Gland, Switzerland.

van Balen, B. (1993) The identification of tit-babblers and red sunbirds on Java. *Oriental Bird Club Bulletin*, **18**, 26–28.

van Balen, B. (1994) Insular ecology of forest bird communities of Java and Bali. *Journal für Ornithologie*, **135** (Suppl.), 210–211.

Balmford, A. (1996) Extinction filters and current resilience: the significance of past selection pressures for conservation biology. *Trends in Ecology and Evolution*, **11**, 193–196.

Bowler, J. & Taylor, J. (1989) An annotated checklist of the birds of Manusela National Park, Seram. Birds recorded on the Operation Raleigh Expedition. *Kukila*, **4**, 3–29.

Brooks, T. & Balmford, A. (1996) Atlantic forest extinctions. *Nature*, **380**, 115.

Brooks, T. & Dutson, G. (1996) Twenty-nine new island records of birds from the Philippines. *Bulletin of the British Ornithologists' Club*, **117**, 32–37.

Brooks, T.M., Evans, T.D., Dutson, G.C.L., Anderson, G.Q.A., Asane, D.C., Timmins, R.J. & Toledo, A.G. (1992) The conservation status of the birds of Negros, Philippines. *Bird Conservation International*, **2**, 273–302.

Brooks, T.M., Pimm, S.L. & Collar, N.J. (1997) Deforestation predicts the number of threatened birds in insular South-east Asia. *Conservation Biology*, **11**, 382–394.

Brown, J.H. (1971) Mammals on mountaintops: nonequilibrium insular biogeography. *American Naturalist*, **105**, 467–478.

Brown, J.H. (1984) On the relationship between abundance and distribution of species. *American Naturalist*, **124**, 255–279.

Butchart, S.H.M., Brooks, T.M., Davies, C.W.N., Dharmaputra, G., Dutson, G.C.L., Lowen, J.C. & Sahu, A. (1996) The conservation status of forest birds on Flores and Sumbawa, Indonesia. *Bird Conservation International*, **6**, 335–370.

Coates, B.J., Bishop, K.D. & Gardner, D. (1997) *A Guide to the Birds of Wallacea*. Dove Publications, Alderley.

Collar, N.J. (1996) The reasons for Red Data Books. *Oryx*, **30**, 121–130.

Collar, N.J. & Long, A.J. (1995) Taxonomy and names of *Carpococcyx* cuckoos from the Greater Sundas. *Forktail*, **11**, 135–150.

Collar, N.J., Crosby, M.J. & Stattersfield, A.J. (1994) *Birds to Watch 2. The World List of Threatened Birds*. BirdLife Conservation Series no. 4. BirdLife International, Cambridge.

Collar, N.J., Wege, D.C. & Long, A.J. (1997) Patterns and causes of endangerment in the New World avifauna. *Ornithological Monographs*, **48**, 237–260.

Collins, N.M., Sayer, J.A. & Whitmore, T.C. (1991) *The Conservation Atlas of Tropical Forests: Asia and the Pacific*. International Union for the Conservation of Nature and Natural Resources. Macmillan Press, London.

Cuarón, A.D. (1993) Extinction rate estimates. *Nature*, **366**, 118.

Daniels, R.J.R. (1996) Landscape ecology and conservation of birds in the Western Ghats, South India. *Ibis*, **138**, 64–69.

Davidson, P., Stones, T. & Lucking, R. (1995) The conservation status of key bird species on Taliabu and the Sula Islands, Indonesia. *Bird Conservation International*, **5**, 1–20.

Davison, G.W.H. (1983) Notes on the extinct *Argusianus bipunctatus* (Wood). *Bulletin of the British Ornithologists' Club*, **103**, 86–88.

Dawning, S.L., Iverson, L.R. & Brown, S. (1993) Rates and patterns of deforestation in the Philippines: application of geographic information system analysis. *Forest Ecology and Management*, **57**, 1–16.

Delacour, J. (1951) *The Pheasants of the World*. Country Life, London.

Diamond, J.M. (1984) 'Normal' extinctions of isolated populations. *Extinctions* (ed. M. H. Nitecki), pp. 191–246. University of Chicago Press, Chicago.

Dickinson, E.C. (1989) A review of the smaller Philippine swiftlets of the genus *Collocalia*. *Forktail*, **5**, 23–34.

Dickinson, E.C., Kennedy, R.S. & Parkes, K.C. (1991) *The Birds of the Philippines*. B.O.U. Check-list no. 12. British Ornithologists' Union, Tring, Herts.

Dutson, G. (1993) A sighting of *Ficedula (crypta) disposita* in Luzon, Philippines. *Forktail*, **8**, 144–147.

Dutson, G. (1995) The birds of Salayar and the Flores Sea Islands. *Kukila*, **7**, 129–141.

Dutson, G.C.L., Magsalay, P.M. & Timmins, R.J. (1993) The rediscovery of the Cebu Flowerpecker *Dicaeum quadricolor*, with notes on other forest birds on Cebu, Philippines. *Bird Conservation International*, **3**, 235–243.

Evans, T.D., Dutson, G.C.L. & Brooks, T.M. (1993) *Cambridge Philippines Rainforest Project 1991: Final*

Report. BirdLife International Study Report no. 54. BirdLife International, Cambridge.

Fraser, B.J. & Henson, S.M. (1996) Survai jenis-jenis burung endemik di Gunung Lompobattang, Sulawesi Selatan [Survey of endemic bird species on Gunung Lompobattang, South Sulawesi]. Technical Memorandum no. 12. PHPA/BirdLife International-Indonesia Programme, Bogor.

Gaston, A.J. & Zacharias, V.J. (1996) The recent distribution of endemic and disjunct birds in Kerala state: preliminary results of an ongoing survey. *Journal of the Bombay Natural History Society*, **93**, 389–400.

Glover, I. (1986) Archeology in eastern Timor, 1966–67. *Terra Australis*, **11**, 1–241.

Gonzales, P.C. & Kennedy, R.S. (1990) A new species of *Stachyris* babbler (Aves: Timaliidae) from the island of Panay, Philippines. *Wilson Bulletin*, **102**, 367–379.

Gonzales, P.C. & Kennedy, R.S. (1996) A new species of *Crateromys* (Rodentia: Muridae) from Panay, Philippines. *Journal of Mammalogy*, **77**, 25–40.

Grayson, D.K. & Livingston, S.D. (1993) Missing mammals on Great Basin mountains: Holocene extinctions and inadequate knowledge. *Conservation Biology*, **7**, 527–532.

Hague, P., Terborgh, J., Winter, B. & Parkinson, J. (1986) Conservation priorities in the Philippine archipelago. *Forktail*, **2**, 83–91.

Harrap, S. & Fisher, T. (1994) A mystery woodcock in the Philippines. *Oriental Bird Club Bulletin*, **19**, 54–56.

Harte, J. & Kinzig, A.P. (1997) On the implications of species-area relationships for endemism, spatial turnover, and food web patterns. *Oikos*, **80**, 417–427.

Heaney, L. (1986) Biogeography of mammals in SE Asia: estimates of rates of colonization, extinction and speciation. *Biological Journal of the Linnean Society*, **28**, 127–165.

Heaney, L.R. (1991) A synopsis of climatic and vegetational change in Southeast Asia. *Climate Change*, **19**, 53–61.

Heaney, L.R. (1997) Philippine mammals: the world's most threatened fauna? *Program and Abstracts* (ed.by American Society of Mammalogists), p. 138. Oklahoma State University, Tulsa.

Heaney, L.R. & Heideman, P.D. (1987) Philippine fruit bats: endangered and extinct. *Bats*, **5**, 3–5.

Heaney, L.R., Heideman, P.D., Rickart, E.A., Utzurrum, R.B. & Klompen, J.S. (1989) Elevational zonation of mammals in the central Philippines. *Journal of Tropical Ecology*, **5**, 259–280.

Holmes, D.A. (1994) A review of the land birds of the West Sumatran Islands. *Kukila*, **7**, 28–46.

ICBP (1992) *Putting Biodiversity on the Map: Priority Areas for Global Conservation*. International Council for Bird Preservation, Cambridge.

Iremonger, S., Ravilious, C. & Quinton, T. (1997) *A Global Overview of Forest Conservation*. CD-ROM. World Conservation Monitoring Centre and Center for International Forestry Research, Cambridge.

van Jaarsveld, A.S., Freitag, S., Chown, S.L., Muller, C., Koch, S., Hull, H., Bellamy, C., Krüger, M., Endrödy-Younga, S., Mansell, M.W. & Scholtz, C.H. (1998) Biodiversity assessment and conservation strategies. *Science*, **279**, 2106–2108.

Janzen, D.H. (1988) Tropical dry forests. The most endangered major tropical ecosystem. *Biodiversity* (ed. E. O. Wilson), pp. 130–137. National Academy Press, Washington, D.C.

Jones, D.N., Dekker, R.W.R.J. & Roselaar, C.S. (1995) *The Megapodes*. Oxford University Press, Oxford.

Jones, M.J., Linsley, M.D. & Marsden, S.J. (1995) Population sizes, status and habitat associations of the restricted-range bird species of Sumba, Indonesia. *Bird Conservation International*, **5**, 21–52.

Kennedy, R.S., Gonzales, P.C. & Miranda, H.C. Jr (1997) New *Aethopyga* sunbirds (Aves: Nectariniidae) from the island of Mindanao, Philippines. *Auk*, **114**, 1–10.

Klop, E., Curio, E. & de Soye, Y. (1998) A new population of bleeding-heart pigeon (*Gallicolumba* sp.) on Panay, Philippines. *Journal für Ornithologie*, **139**, 76–77.

Krummel, J.R., Gardner, R.H., Sugihara, G., O'Neill, R.V. & Coleman, P.R. (1987) Landscape patterns in a disturbed environment. *Oikos*, **48**, 321–324.

Lambert, F. (1994) Notes on the avifauna of Bacan, Kasiruta and Obi, North Moluccas. *Kukila*, **7**, 1–9.

Lambert, F. (1998) A new species of *Gymnocrex* from the Talaud Islands, Indonesia. *Forktail*, **13**, 1–6.

Lambert, F. & Woodcock, M. (1996) *Pittas, Broadbills and Asities*. Pica Press, Robertsbridge.

Lambert, F. & Yong, D. (1989) Some recent bird observations from Halmahera. *Kukila*, **4**, 30–33.

Laurance, W.F., Birregaard, R.O. Jr, Gascon, C., Didham, R.K., Smith, A.P., Lynam, A.J., Viana, V.M., Lovejoy, T.E., Sieving, K.E., Sites, J.W. Jr, Andersen, M., Tocher, M.D., Kramer, E.A., Restrepo, C. & Moritz, C. (1997) Tropical forest fragmentation: synthesis of a diverse and dynamic discipline. *Tropical Forest Fragments* (eds W. F. Laurance & R. O. Bierregaard, Jr), pp. 502–514. University of Chicago Press, Chicago.

Lazell, J. (1992) New flying lizards and predictive biogeography of two Asian archipelagos. *Bulletin of the Museum of Comparative Zoology*, **152**, 475–505.

MacArthur, R.H. & Wilson, E.O. (1967) *The Theory of Island Biogeography*. Princeton University Press, Princeton.

MacArthur, R.H., Diamond, J.M. & Karr, J.R. (1972) Density compensation in island faunas. *Ecology*, **53**, 330–342.

McGregor, R.C. (1920) Some features of the Philippine ornis with notes on the vegetation in relation to the avifauna. *Philippine Journal of Science*, **16**, 361–437.

Mackinnon, J. & Phillipps, K. (1993) *A Field Guide to the Birds of Borneo, Sumatra, Java and Bali*. Oxford University Press, Oxford.

Madge, S. & Burn, H. (1993) *Crows and Jays*. Christopher Helm, London.

Marsden, S.J., Jones, M.J., Linsley, M.D., Mead, C. & Hounsome, M.V. (1997) The conservation status of the restricted-range lowland birds of Buru, Indonesia. *Bird Conservation International*, **7**, 213–234.

Mees, G.F. (1995) On *Malacocincla vanderbilti* de Schauensee & Ripley, and *Malacocincla perspicillata* (Bonaparte) (Aves, Timaliidae). *Proceedings of the Koninklijke Nederlandse Akademie Van Wetenschappen*, **98**, 63–68.

Moeliker, C.W. & Heij, C.J. (1995) The rediscovery of *Monarcha boanensis* (Aves: Monarchidae) from Boano Island, Indonesia. *Deinsea*, **2**, 123–143.

Morris, P. (1996) Sightings of an unusual, possibly new shortwing in the Philippines. *Oriental Bird Club Bulletin*, **23**, 55.

Murcia, C. (1995) Edge effects in fragmented forests: implications for conservation. *Trends in Ecology and Evolution*, **10**, 58–62.

Musser, G.G. (1981) The giant rat of Flores and its relatives east of Borneo and Bali. *Bulletin of the American Museum of Natural History*, **169**, 67–176.

Musser, G.G. (1987) The mammals of Sulawesi. *Biogeographical Evolution of the Malay Archipelago*

(ed. T. C. Whitmore), pp. 73–93. Clarendon Press, Oxford.

Myers, N. (1994) Tropical deforestation: rates and patterns. *The Causes of Tropical Deforestation* (eds K. Brown & D. W. Pearce), pp. 27–40. University College Press, London.

O'Brien, T.G. & Kinnaird, M.F. (1996) Changing populations of birds and mammals in North Sulawesi. *Oryx*, **30**, 150–156.

Oliver, W.L.R. (1994) Threatened endemic mammals of the Philippines: an integrated approach to the management of wild and captive populations. *Creative Conservation: Interactive Management of Wild and Captive Animals* (eds P. J. S. Olney, G. M. Mace & A. T. C. Feistner), pp. 467–477. Chapman & Hall, London.

Olson, S.L. (1986) *Gallirallus sharpei* (Büttikofer), nov. comb. A valid species of rail (Rallidae) of unknown origin. *Gerfaut*, **76**, 263–269.

Parkes, K.C. (1992) [Review of] Distribution and taxonomy of birds of the world. *Journal of Field Ornithology*, **63**, 228–235.

Payne, J., Francis, C.M. & Phillipps, K. (1985) *A Field Guide to the Mammals of Borneo*. The Sabah Society, Kota Kinabalu.

Pimm, S.L. (1991) *The Balance of Nature?* Chicago University Press, Chicago.

Pimm, S.L. & Askins, R.A. (1995) Forest losses predict bird extinctions in eastern North America. *Proceedings of the National Academy of Sciences of the U.S.A.*, **92**, 9343–9347.

Pimm, S.L., Moulton, M.P. & Justice, L.J. (1994) Bird extinctions in the central Pacific. *Philosophical Transactions of the Royal Society of London B*, **344**, 27–33.

Pimm, S.L., Russell, G.J., Gittleman, J.L. & Brooks, T.M. (1995) The future of biodiversity. *Science*, **269**, 347–350.

Poulson, M.K. (1995) The threatened and near-threatened birds of Luzon, Philippines, and the role of the Sierra Madre mountains in their conservation. *Bird Conservation International*, **5**, 79–116.

Preston, F.W. (1962) The canonical distribution of commonness and rarity. *Ecology*, **43**, 185–215, 410–432.

Rabor, D.S. (1959) The impact of deforestation on birds of Cebu, Philippines, with new records for that island. *Auk*, **76**, 37–43.

Renjifo, L.M., Servat, G.P., Goerck, J.M., Loiselle, B.A. & Blake, J.G. (1997) Patterns of species composition and endemism in the northern Neotropics: a case for conservation of montane avifaunas. *Ornithological Monographs*, **48**, 577–594.

RePPProT (1990) *National Overview of the Regional Physical Planning Programme for Transmigration*. Overseas Development Natural Resources Institute, Chatham.

Restall, R.L. (1996) A proposed new species of munia, genus *Lonchura* (Estrildinae). *Bulletin of the British Ornithologists' Club*, **116**, 137–142.

Rhind, J. & Iremonger, S. (1996) *Tropical Moist Forests and Protected Areas: the Digital Files*. World Conservation Monitoring Centre and Center for International Forestry Research, Cambridge.

Riley, J. (1997) The birds of Sangihe and Talaud. *Kukila*, **9**, 3–36.

Rosenzweig, M.L. (1995) *Species Diversity in Space and Time*. Cambridge University Press, Cambridge.

Rozendaal, F.G. (1990) Vocalizations and taxonomic status of *Caprimulgus celebensis*. *Dutch Birding*, **12**, 79–81.

Rozendaal, F.G. (1994) Species limits within the Garnet Pitta-complex. *Dutch Birding*, **16**, 239–245.

Russell, G.J., Brooks, T.M., McKinney, M.L. & Anderson, C.G. (1998) Present and future taxonomic selectivity in bird and mammal extinctions. *Conservation Biology*, **12**, 1365–1376.

Shahabuddin, G. (1997) Preliminary observations on the role of coffee plantations as avifaunal refuges in the Palni Hills of the Western Ghats. *Journal of the Bombay Natural History Society*, **94**, 10–21.

Sibley, C.G. & Monroe, B.L. Jr (1990) *Distribution and Taxonomy of Birds of the World*. Yale University Press, Newhaven.

Sibley, C.G. & Monroe, B.L. Jr (1993) *A Supplement to Distribution and Taxonomy of Birds of the World*. Yale University Press, Newhaven.

Smiet, F. (1985) Notes on the field status and trade of Moluccan parrots. *Biological Conservation*, **34**, 181–194.

Spiegel, M.R. (1994) *Theory and Problems of Statistics*. 2nd edn. McGraw-Hill, Inc., New York.

SSC (1988) *Mapping the Natural Conditions of the Philippines*. Swedish Space Corporation, Stockholm.

Stattersfield, A.J., Crosby, M.J., Long, A.J. & Wege, D.C. (1998) *Endemic Bird Areas of the World: Priority Areas for Biodiversity Conservation*. BirdLife Conservation Series no. 7. BirdLife International, Cambridge.

Terborgh, J. (1974) Preservation of natural diversity: the problem of extinction prone species. *Bioscience*, **24**, 715–722.

Terborgh, J. (1977) Bird species diversity on an Andean elevational gradient. *Ecology*, **58**, 1007–1019.

Tobias, J. (1995) Birdwatching areas. Kerinci-Seblat National Park, Sumatra. *Oriental Bird Club Bulletin*, **25**, 53–57.

White, C.N.M. & Bruce, M.D. (1986) *The Birds of Wallacea*. B.O.U. Check-list no. 7. British Ornithologists' Union, Tring, Herts.

Whitmore, T.C. (1984) *Tropical Rain Forests of the Far East*. Clarendon Press, Oxford.

Whitmore, T.C. (1997) Tropical forest disturbance, disappearance, and species loss. *Tropical Forest Remnants* (eds W. F. Laurance & R. O. Bierregaard, Jr), pp. 3–12. Chicago University Press, Chicago.

Whitten, A.J., Bishop, K.D., Nash, S.V. & Clayton, L. (1987) One or more extinctions from Sulawesi, Indonesia. *Conservation Biology*, **1**, 42–48.

Wilson, D.E. & Reeder, D.M. (1993) *Mammal Species of the World. A Taxonomic and Geographic Reference*. Smithsonian Institution Press, Washington, D.C.

With, K.A. (1997) The application of neutral landscape models in conservation biology. *Conservation Biology*, **11**, 1069–1080.

Appendix 1

Forest cover data for South-east Asian islands and archipelagos. Total area and forest area are in km²; edge (length of the forest–nonforest perimeter) is in km. For sources, see text.

Island	Total %	Area	Forest	Montane %	Area	Forest	Edge	Lowland %	Area	Forest	Edge
Luzon	25	109 431	26 913	61	11 533	7035	12 508	20	97 898	19 580	37 494
Mindoro	10	10 059	1009	29	1323	384	1638	7	8736	612	3055
Western Visayas	7	26 729	1799	64	999	636	1165	5	25 730	1171	4351
Cebu	0	4661	0	0	15	0	0	0	4661	0	0
Mindanao	29	123 974	35 684	69	12 082	8326	11 107	24	111 895	27 265	57 161
Sulus	4	3534	133	–	0	–	–	4	3534	141	492
Palawan	50	14 842	7465	96	401	385	143	49	14 441	7076	12 526
Flores	15	33 961	5147	44	3395	1504	4668	12	30 566	3644	2600
Sumba	12	10 762	1296	47	125	59	644	12	10 637	1237	411
Timor	14	31 561	4295	21	3309	682	3127	13	5213	4168	1629
Java	10	136 833	13 642	50	13 091	6496	23 174	6	123 741	7164	42 303
Borneo	72	738 262	531 406	92	27 900	25 593	7185	71	710 361	505 814	387 200
Sumatra	50	452 722	224 219	74	52 119	38 605	39 889	46	400 603	185 613	387 219
West Sumatran Is.	56	11 416	6442	–	0	–	–	56	11 416	6442	7678
Sulawesi	61	187 831	116 143	86	37 571	32 382	20 352	55	150 261	83 761	118 343
Far Moluccas	≈5	'Virtually none'	–	–	0	–	–	≈5	'Virtually none'	–	–
Halmahera	86	26 826	23 018	95	495	472	21	86	26 331	22 546	16 165
Buru	77	8613	6671	96	1791	1720	430	73	6822	4951	6514
Seram	82	19 036	15 549	98	1097	1078	239	81	17 939	14 472	15 420
PHILIPPINES	25	293 230	73 003	64	26 353	16 766	26 561	21	266 880	55 836	115 079
LESSER SUNDAS	18	81 560	14 906	33	6829	2245	8281	17	74 731	12 663	37 666
GREATER SUNDAS	58	1 339 233	775 709	76	93 110	70 694	70 248	57	1 246 121	705 033	824 400
NORTH WALLACEA	67	242 306	161 381	87	40 954	35 652	21 042	62	201 353	125 730	153 335

Appendix 2

Endemic birds of South-east Asian islands. See text for data sources. Single-island values are the sums of those for all islands within an archipelago. Totals for each archipelago are the sum of the single-island values and those for species endemic to but widespread within the archipelago. These are the values that were used in Table 1.

Island	All species			Montane species			Lowland species		
	Endemic	Threatened	Predicted	Endemic	Threatened	Predicted	Endemic	Threatened	Predicted
Luzon	25	11	7·3	8	6	0·9	17	5	5·6
Mindoro	6	6	2·6	2	2	0·5	4	4	1·9
Western Visayas	9	9	4·4	3	3	0·3	6	6	3·2
Cebu	3	3	3·0	0	0	0·0	3	3	3·0
Mindanao	37	17	9·8	17	9	1·5	20	8	6·0
Sulus	3	3	1·7	—	—	—	3	3	1·7
Palawan	37	6	2·7	2	0	0·0	15	6	2·5
Single-island	100	55	31·5	32	20	3·3	68	35	23·8
Widespread	82	16	24·0	12	3	1·3	70	13	22·7
PHILIPPINES	182	71	55·5	44	23	4·6	138	48	46·5
Flores	16	3	6·0	6	2	1·1	10	1	4·1
Sumba	8	3	3·3	1	1	0·2	7	2	2·9
Timor	21	5	8·2	1	1	0·3	20	4	8·0
Banda Sea Is.	23	0	1·2	—	—	—	23	0	1·2
Single-island	68	11	18·7	8	4	1·6	60	7	16·2
Widespread	18	1	6·3	4	0	1·0	14	1	5·0
LESSER SUNDAS	86	12	25·0	12	4	2·6	74	8	21·2
Java	27	5	11·8	17	2	2·7	10	4	5·1
Borneo	38	3	3·0	28	0	0·6	10	3	0·8
Sumatra	15	7	2·4	14	6	1·0	1	1	0·2
West Sumatran Is.	4	0	0·5	—	—	—	4	0	0·5
Single-island	84	15	17·7	59	7	4·3	25	8	6·6
Widespread	27	2	3·4	21	1	1·4	6	1	6·0
GREATER SUNDAS	111	17	21·2	80	8	5·7	31	9	12·6
Sulawesi	86	5	10·0	29	1	1·1	57	4	7·9
Far Moluccas	5	4	2·6	—	—	—	5	4	2·6
Halmahera	29	5	1·1	3	1	0·0	26	4	1·0
Buru	10	2	0·6	5	0	0·1	5	2	0·4
Seram	15	4	0·9	5	1	0·0	10	3	0·5
Single-island	145	20	15·3	42	3	1·2	103	17	12·4
Widespread	21	1	2·0	5	0	0·2	16	1	1·8
NORTH WALLACEA	166	21	17·3	47	3	1·4	119	18	14·2

Appendix 3

Endemic mammals of South-east Asian islands. See text for data sources. We obtained overall values for each archipelago in the same way as for birds (Appendix 2) and used these values in Table 2.

Island	All species			Montane species			Lowland species		
	Endemic	Threatened	Predicted	Endemic	Threatened	Predicted	Endemic	Threatened	Predicted
Luzon	22	9	6·4	16	5	1·9	6	4	2·0
Mindoro	6	5	2·6	3	3	0·8	3	2	1·5
Western Visayas	4	3	1·9	1	1	0·1	3	2	1·6
Cebu	0	0	0·0	0	0	0·0	0	0	0·0
Mindanao	29	9	7·7	13	5	1·2	16	4	4·8
Sulus	1	1	0·6	—	—	—	1	1	0·6
Palawan	16	7	2·5	2	2	0·0	14	5	2·3
Single-island	78	34	21·8	35	16	3·9	43	18	12·7
Widespread	22	5	6·4	4	0	0·4	18	5	5·8
PHILIPPINES	100	39	28·3	39	16	4·4	61	23	18·5
Flores	9	6	3·4	1	0	0·2	8	6	3·3
Sumba	0	0	0·0	0	0	0·0	0	0	0·0
Timor	6	3	2·3	1	0	0·3	5	3	2·0
Banda Sea Is.	1	1	0·1	—	—	—	1	1	0·1
Single-island	16	10	5·8	2	0	0·5	14	10	5·3
Widespread	4	0	1·4	0	0	0·0	4	0	1·4
LESSER SUNDAS	20	10	7·2	2	0	0·5	18	10	6·8
Java	19	4	8·3	10	2	1·6	9	2	4·5
Borneo	49	13	3·9	28	10	0·6	21	3	1·7
Sumatra	16	5	2·5	9	4	0·7	7	1	1·2
West Sumatran Is.	18	7	2·4	—	—	—	18	7	2·4
Single-island	102	29	17·2	47	16	2·8	55	13	9·9
Widespread	12	3	1·5	3	1	0·2	9	2	1·2
GREATER SUNDAS	114	32	18·7	50	17	3·0	64	15	11·1
Sulawesi	72	22	8·4	31	18	1·1	41	4	5·7
Far Moluccas	1	0	0·5	—	—	—	1	0	0·5
Halmahera	6	1	0·2	1	1	0·0	5	0	·2
Buru	0	0	0·0	0	0	0·0	0	0	0·0
Seram	6	0	0·4	5	0	0·0	1	0	0·1
Single-island	85	23	9·5	37	19	1·2	48	4	6·5
Widespread	8	2	0·9	0	0	0·0	8	2	0·9
NORTH WALLACEA	93	25	10·3	37	19	1·2	56	6	7·4