Biodiversity and Conservation **11**: 695–704, 2002.

Endemism, diversity, and the threat of tropical moist forest extinctions

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Received 28 August 2000; accepted in revised form 2 May 2001

Abstract. Extinction rates have risen to perhaps 10^4 the background rate. Much of this increase is due to projected influences of habitat loss on regions of the world with tropical moist forest. This ecosystem, home to a disproportionate amount of global biodiversity and a major regulator of regional and global climate, also faces disproportionately severe threats. In this study, we collect diversity and endemism data for tropical forested countries of the world, along with areal and socioeconomic data. While a correlation between overall numbers of species and endemic species per country is expected, we demonstrate that endemism patterns among birds and mammals remain very strongly convergent even after statistically rendering all countries equal in size and overall species richness and after adjusting for spatial autocorrelation. On a per country basis, mammals are generally more threatened than birds in these tropical moist forested countries. Human population growth rates and rising debt among these nations should be viewed as priorities for amelioration by the developed countries. Reserve network extent is not related to numbers of endemic mammals or birds at this large spatial scale.

Key words: endemic species, protected areas, threatened species, tropical forests

Introduction

Many of the world's hotspots for animal diversity are found in nations with tropical moist forests, but these nations also face profound socioeconomic difficulties that cause widespread habitat loss and degradation. Largely as a result of such difficulties in tropical countries, human-induced extinctions are occurring at perhaps 10^4 times the natural, background rate (May and Tregonning 1998). While there is now significant documentation of spatial patterns of biodiversity at a range of spatial scales (Kerr and Packer 1997; Mittermeier 1988; Myers 1988, 1990; Pimm and Raven 2000), major gaps in understanding of these patterns plague efforts to direct limited conservation funding. Funding through 'megadiversity country' initiatives and complementary hotspot analyses will continue to be important in resolving this problem (e.g. Myers et al. 2000). There is an acute need to direct conservation efforts toward those regions, typically in the tropics and in global biodiversity hotspots, where there are particularly large numbers of endemic and threatened species (May and

Tregonning 1998). Substantial gaps in our understanding of patterns of endemism, species richness, and threatened species distributions in tropical countries jeopardize the success of international conservation efforts, though systematic efforts begin to address this deficiency (Kerr 2001a; Mittermeier et al. 1999).

New statistical analyses of the world's hotspots have further elaborated the importance of these zones to global conservation success. Perhaps 44% of all vascular plants, and as much as 35% of vertebrate species are confined to the hotspot regions identified by Myers (1988, 1990) and later refined by Myers et al. (2000). The 25 hotspots identified by iterations of this prioritization process comprise only about 1.4% of the world's land area, so it is at least theoretically possible to make enormous strides in conserving global biodiversity by directing action to these areas. The concentration of biodiversity in a small area can facilitate conservation efforts or increase the likelihood of an even more rapid, mass extinction. Almost 20% of the global population live in biodiversity hotspot regions (identified as covering 12% of world land area; Cincotta et al. 2000). Furthermore, Cincotta et al. (2000) point out that population growth rates in these areas are higher than either global or developing world averages. Deterioration of biodiversity hotspots can be expected to continue or even accelerate, at least over the short term.

We examine patterns of endemism and numbers of threatened birds and mammals solely among the 42 countries with tropical moist forests. We restrict our investigation to these countries alone because global comparisons of endemism rates most frequently note that endemism in these places is high relative to temperate and cold regions of the world (e.g. Ceballos and Brown 1995; Kerr and Currie 1995). Here, we explore the link between endemism and magnitude of extinction threat after adjusting for obscuring influences such as overall diversity (e.g. latitudinal gradients of species richness), area, and after adopting a conservative stance with respect to spatial autocorrelation (SA). We also investigate the link between extent of protected area in countries with tropical moist forest and the degree of threat facing their mammal and bird biotas, respectively.

Methods

We collected data on species richness, numbers of threatened and endemic species of birds and mammals, country size, and extent of protected area for all countries with tropical moist forests (World Conservation Monitoring Centre and World Conservation Union 1996; World Resources Institute 1998). There are approximately 42 such countries. Our list includes Bangladesh, Belize, Benin, Bolivia, Brazil, Burundi, Cameroon, Central African Republic, Colombia, Congo, Costa Rica, Côte D'Ivoire, Dominican Republic, Ecuador, El Salvador, Equatorial Guinea, French Guiana, Gabon, Ghana, Guatemala, Guyana, Haiti, Honduras, India, Indonesia, Madagascar, Malaysia, Mexico, Nicaragua, Nigeria, Panama, Papua New Guinea, Peru, Philippines, Rwanda, Sri Lanka, Suriname, Thailand, Togo, Uganda, Venezuela, and Zaire (Democratic Republic of Congo). Endemic species are those found only in one country and threatened species are listed in the IUCN Red List of Threatened Animals. Threatened status is reserved for species that are at global risk of extinction, stratified as critically endangered, endangered, or vulnerable. Some species are considered to be too poorly known ('data deficient'), have not been evaluated, or are known or strongly believed to be extinct: these are excluded from our analysis. Many species listed as globally threatened persist in more than one country, so our results cannot be extrapolated to provide estimates of total numbers of threatened birds or mammals in tropical countries with moist forest. Overall species richness for each of the study countries is derived from numerous sources that have been integrated at WCMC to provide a measurement of countrywide biodiversity for the best collected taxa. These data are of variable quality. The unit of analysis for our study (the country) should be sufficiently coarse to render errors in the diversity data relatively small. Our results, which do not seem in any way to be consistent with a sampling effect or random error, support this conclusion. Nevertheless, we caution that tropical biodiversity data is far less reliable than those for temperate regions. Efforts are underway to improve collaboration among various research groups to create a more synthetic global biodiversity database (Kerr 2001a).

Protected area per country includes zones that fall within IUCN protected areas categories I–V. We also collected human population growth and foreign debt data for countries with particularly large numbers of threatened and endemic bird and mammal species. Foreign debt load is calculated using the World Bank Atlas method, and is a three-year average expressed in US$ and adjusted for domestic and US inflation. Three-year averaging of the index adjusts for fluctuations in monetary exchange rates.

Because area generally influences diversity (Ceballos and Brown 1995), we regressed species richness and numbers of threatened and endemic bird and mammal species per country, respectively, against country size and used residuals for further analyses. After examining bivariate plots of the variables to determine if regression assumptions were likely to be violated by further analysis, we calculated linear regressions reported above, following standard methods in the discipline (e.g. Ceballos and Brown 1995).

Biodiversity data almost always exhibit SA (Kerr 2001b). SA is the tendency for data points that are near to one another to be more similar than those that are widely separated. SA, when present among study data, violates the assumption of the independence of data values of the response variable in statistical analyses such as least squares linear regression. Violation of the independence assumption in regression analyses causes increased probability of rejecting the null hypothesis when the null hypothesis is actually true by inflating the number of degrees of freedom available for the analysis. This is Type I statistical error, and it can be remedied by adopting a very conservative stance with respect to the number of degrees of freedom in the statistical analysis. This is the canonical approach to addressing SA among ecological data (see

Koenig 1999 for a broader discussion of SA in ecology; see Kerr et al. 2000 and Kerr 2001b for examples of tests for SA among analagous biodiversity data; Sokal and Oden 1978a, b discuss methods of detecting SA). We adopted the conservative stance recommended for assessing numbers of degrees of freedom in analyses of spatially autocorrelated data. We also discuss the possible influence of SA with each of our results reported below, and the minimum number of degrees of freedom that must be present to detect significance in our data. While still reporting probability values for all analyses, in keeping with properly transparent statistical reporting, we urge caution in attempts to interpret those values. The magnitudes of the correlations we have discovered are of more direct interest.

Results and discussion

After correcting for country size, there is very strong covariation between numbers of endemic mammal and bird species in the countries we have studied ($F = 256.7$, $P \ll 0.0001$, adjusted $R^2 = 0.86$; Figure 1). We discover a similar pattern when endemism is measured as the proportion of endemic to overall bird or mammal species richness per country, respectively (after adjusting for land area, $F = 1210$, $P \ll 0.0001$, adj. $R^2 = 0.97$). This suggests that similar biological forces act to create centres of tropical endemism among both birds and mammals, and that conservation efforts in these 'hotspot' countries should be particularly valuable. Invertebrate and plant endemism and richness patterns do not necessarily reflect those of birds or mammals, particularly at finer scales, so these results may not apply generally to other taxa (Kerr 1997; Prendergast et al. 1993; Reid 1998). Our results do not support previous findings (Ceballos and Brown 1995) that showed that international patterns of endemism and richness do not covary. Previous results were based on a larger sample of countries and did not focus solely on tropical, forested countries which house most terrestrial biological diversity. The co-mingling of very different countries across climatic and biotic regions may have obscured detectable relationships within tropical 'megadiversity countries'. Our results focus on the subset of countries where diversity is thought to be concentrated, and where socioeconomic conditions are particularly unfavourable to future conservation efforts.

There is striking overlap between the extent to which mammal and bird biotas (proportion of species currently threatened at a national level, corrected for land area) are threatened with extinction in tropical moist forested countries ($F = 57.5$, $P \ll 0.0001$, adj. $R^2 = 0.59$). These data suggest that similar aspects of human activity influence extinction risk among birds and mammals in tropical moist forested countries (Wright 1987; Kerr and Currie 1995).

There are more nationally threatened birds and mammals in countries with large numbers of endemic species for the taxon (birds: $F = 39.0$, adj. $R^2 = 0.49$, $P \ll 0.0001$; mammals: $F = 10.4$, adj. $R^2 = 0.19$, $P = 0.0025$), also contrary to

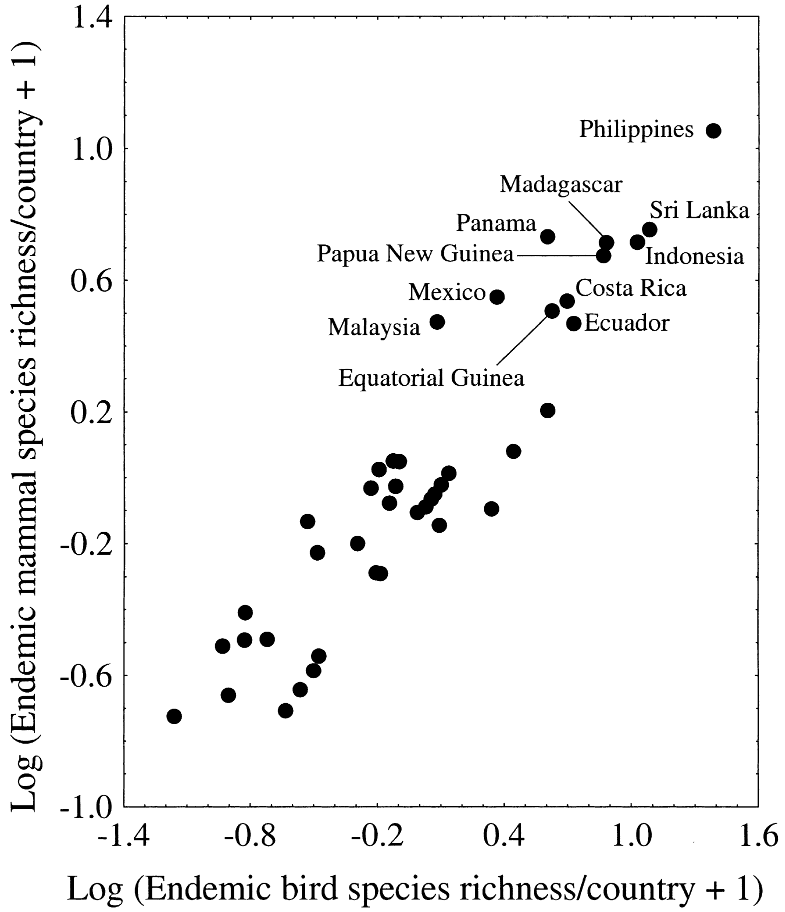

Figure 1. The relationship between number of endemic mammals and birds in countries with tropical moist forests after adjusting for country area.

some earlier international-scale findings (Ceballos and Brown 1995). Philippines, Madagascar, Indonesia, Brazil, Papua New Guinea, and Mexico have particularly high proportions endemic species and face the greatest threats to their biodiversity, even after controlling for country size. The ultimate causes of the convergent threat to biodiversity in these regions is likely to rest with their rapidly changing socioeconomic position. The respective socioeconomic conditions in these countries seem increasingly precarious: annual population growth rates range from 1.2 to 3.1% (World Resources Institute 1998). From 1985 to 1995, foreign debt loads in these countries increased by 39–200%, a factor that is likely to have exacerbated recent economic turmoil in most of these countries. Heavier debt loads also reduce these nations' ability to dedicate economic resources to conservation programs and address the underlying social factors causing the present extinction crisis (World Resources

Institute 1998). International debt relief initiatives, such as the ongoing Heavily Indebted Poor Countries (HIPC; van Trotsenburg and MacArthur 1999) Initiative or Jubilee 2000 (e.g. http://www.jubilee2000uk.org/), may lessen some of these problems but the conservation results of debt relief that has arrived to date remains unknown.

Mammals are at greater risk than birds in these countries, with consistently higher proportions threatened ($t = 2.91$, $P < 0.005$; mean percent threatened: mammals = 9.6% and birds = 2.6%). A plot of percent threatened mammals vs. percent threatened birds (that is, numbers of threatened bird or mammal species divided by bird or mammal species richness in each country) has a slope of 1.32, and a y-intercept of 0.04 (Figure 2). Mammals also face a consistently greater threat than birds, indicating

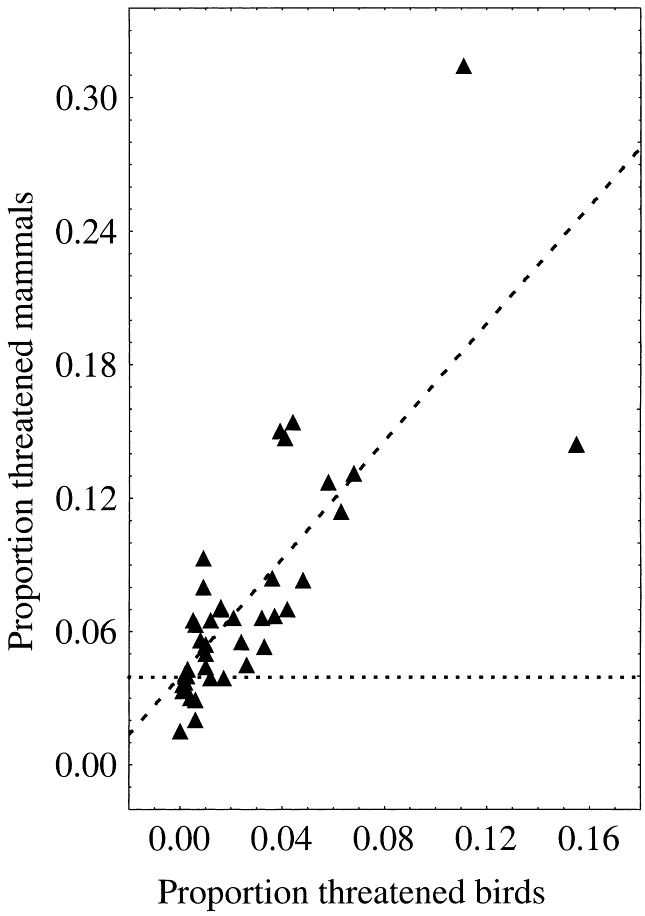

Figure 2. Proportions of threatened bird and mammal species per country are strongly related. The horizontal dotted line shows the location of the x-intercept, located at 0.04. In general, therefore, 4% of tropical forested country's mammal fauna is threatened with extinction before any birds are listed. This is one way to gauge the different conservation status of these taxa.

that mammals are particularly sensitive to environmental perturbations occurring in this region. This may be attributable to their larger mean body sizes, a common correlate of extinction risk (Arita et al. 1990; Bown et al. 1994; Gaston and Blackburn 1995; Pimm et al. 1989), correspondingly greater area requirements, and lower vagility. Other studies have often found strong correlations between body size and extinction risk. Habitat loss and fragmentation are likely primary causes of extinction (Balmford and Long 1995; Burkey 1995, 1997; Tilman et al. 1994) among both taxa, while overhunting and the pet trade (Collar et al. 1994) are likely to affect birds and mammals to differing extents. Birds are monitored more closely than mammals and it is possible that we observe this pattern because of the application of a precautionary principle in assessing mammal status. However, we consider this an unlikely explanation of this finding, given that others have independently found very low populations densities among many mammal taxa in different tropical forest habitats (Bodmer et al. 1997).

Endemics, which by definition have restricted ranges, appear to face a disproportionately high extinction risk (Fox et al. 1996) in tropical moist forested countries, and current systems of reserves are likely inadequate for species conservation needs when measured at this international scale. In other words, areas of the world with many endemic species face particularly severe threat. More broadly, even among these highly diverse tropical forested nations, there are significant gradients of diversity, endemism, and degree of threat that are independent of these countries' areal extent.

We also find that extent of protected area in the sampled countries does not correspond well with either the number of endemic or threatened species per country, after controlling for land area (Figure 3). This finding is consistent with other results that show that many reserves are too small to provide adequate protection for vertebrates (Fox et al. 1996; Newmark 1986, 1995) and that, at an international scale, reserve networks do not seem to affect numbers of threatened species in a country. An additional factor that may affect this relationship is that many reserves in the tropics receive little practical protection (Peres and Terborgh 1995), a problem that is likely exacerbated by the relatively high accessibility of many tropical parks. Moreover, it seems that parks are established for such a diversity of reasons that one would not necessarily expect the extent of reserves in a country to correlate with its concentration of threatened or endemic species. While reserve selection algorithms are very powerful (e.g. Rodrigues et al. 2000), these are almost never used; reserve networks are rarely planned at a national scale, and are most frequently established opportunistically. For instance, reserves are established for their scenic beauty and often for historical reasons such as the presence of an older hunting reserve. Furthermore, large reserves are often established where the opportunity costs are low (e.g. deserts and arid areas, mountain regions or arctic tundra, remote and inaccessible areas) rather than where the biological importance might be the highest. On the other hand, it may be that large protected areas and protected areas networks do play an important role in the conservation of threatened or endemic species at present but that this relationship

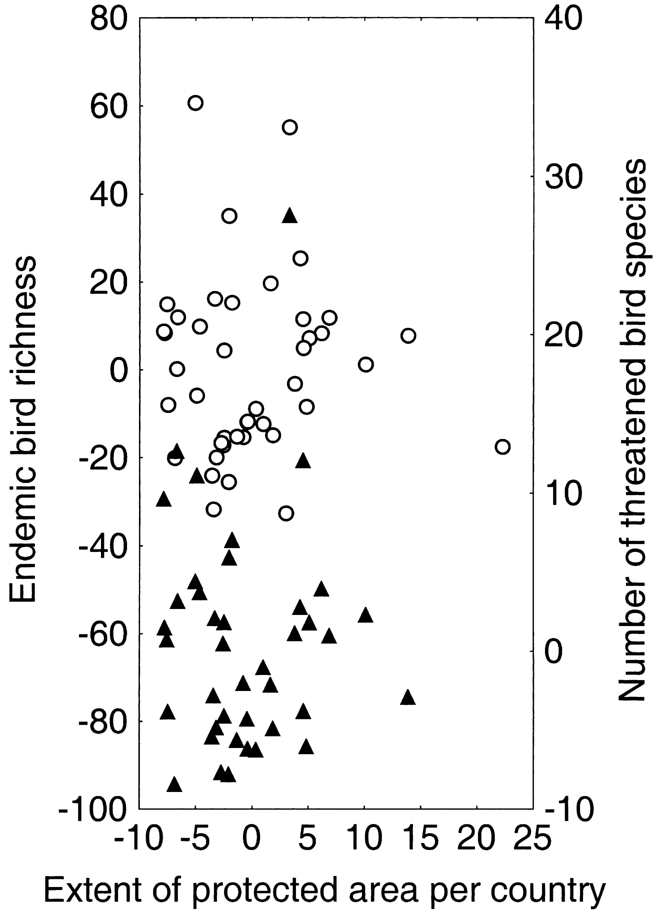

Figure 3. The relationships between both numbers of endemic and threatened bird species per country and extent of protected area (proportion of total country area protected) after adjusting for country size. This reflects human influence rather than area effects, which are of secondary interest. Open circles denote endemic bird species per country, while filled triangles represent numbers of threatened bird species per country. Similar results obtain when numbers of threatened and endemic mammals per country are plotted against extent of protected area.

is obscured in our analysis. For instance, some countries may have few threatened species because they have large reserve systems while other countries may have large reserve systems (recently established) because they have many threatened or endangered species. Yet other countries may have large reserve systems and few threatened or endangered species because the opportunity costs for the land are low and there are few developments threatening or encroaching upon important habitats (e.g. countries with large, inaccessible forest tracts and limited infrastructure).

Unfortunately, human activities threaten biological diversity disproportionately in countries which are most important for global conservation efforts, while socioeconomic conditions in these countries remain precarious or are deteriorating (Ehrlich et al. 1995; Sisk et al. 1994). In a climate of competition for funds among numerous causes and interests, we suggest that one might get more conservation 'bang for your buck' by focussing efforts where the concentrations of threatened and endemic species are the highest – weighted, possibly, by the chances of success in a given area and/or the imminence of the threat that it may face.

Acknowledgements

TVB acknowledges post-doctoral support from the Norwegian Research Council. JTK is grateful for Natural Sciences and Engineering Research Council of Canada doctoral and post-doctoral fellowships. Robert May, Paul Harvey, and Georgina Mace made many helpful comments on this manuscript as did two anonymous reviewers. This research is supported in part by operating funds from the Royal Society and Wellcome Trust to Robert May and an NSERC grant to L. Packer.

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