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How global extinctions impact regional biodiversity in mammals

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Phylogenetic diversity (PD) represents the evolutionary history of a species assemblage and is a valuable measure of biodiversity because it captures not only species richness but potentially also genetic and functional diversity. Preserving PD could be critical for maintaining the functional integrity of the world's ecosystems, and species extinction will have a large impact on ecosystems in areas where the ecosystem cost per species extinction is high. Here, we show that impacts from global extinctions are linked to spatial location. Using a phylogeny of all mammals, we compare regional losses of PD against a model of random extinction. At regional scales, losses differ dramatically: several biodiversity hotspots in southern Asia and Amazonia will lose an unexpectedly large proportion of PD. Global analyses may therefore underestimate the impacts of extinction on ecosystem processes and function because they occur at finer spatial scales within the context of natural biogeography.

Keywords: phylogenetic diversity; biodiversity; threatened species; mammals; extinction

1. INTRODUCTION

Phylogenetic diversity (PD; [1]) has been suggested as a valuable measure of biodiversity because it not only takes into account species richness but could also reflect genetic and functional diversity [2–4]. Therefore, potential PD loss may provide an index of ecological vulnerability. Recently, Fritz & Purvis [5] demonstrated dramatic geographical variations in potential PD loss across terrestrial ecoregions. However, we still lack spatially explicit models describing the patterns of potential PD loss at the finer scales more relevant to practical conservation. In addition, the mechanisms explaining differences in PD loss remain poorly understood. Using a complete phylogeny [6] and a comprehensive range database for terrestrial mammals [7], we estimate impacts of global extinctions at a finer spatial scale than used conventionally in global studies [2,8] and provide novel insights into species' conservation values.

Knowledge of regional extinction patterns is important for developing strategies to conserve biodiversity. First,

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threatened mammal species richness varies dramatically across space [7,8]. Second, many drivers of extinction risk are shown to be geographically restricted, including environmental factors and anthropogenic disturbance [6,9]. Finally, the loss of particular species can impact different communities or ecosystems differently necessitating geographically specific assessment.

There are two non-exclusive mechanisms that explain high PD loss. First, species on longer terminal branches may be at higher risk of extinction than those subtending from shorter branches [10]. Species on longer branches are considered more evolutionarily distinct because they have no close relatives. At the global scale, such species have been termed evolutionarily distinctive globally endangered (EDGE; [11]), and have attracted attention of conservationists in the past decade [11–13]. Alternatively, species might have close relatives in other regions but be locally distinct. Second, if factors that increase species extinction risk are phylogenetically clumped, then PD loss may be high because we risk losing the internal branches connecting the species [14,15]. Phylogenetic structure in extinction risk has recently been demonstrated globally in mammals [16] but has never been assessed in a geographical context.

Here, we present, to our knowledge, the first global assessment of potential PD loss to focus on geographical patterns and mechanisms at regional scales. We (i) compare PD loss owing to extinctions of threatened species with a global random extinction model; (ii) identify localities with higher PD loss than expected from regionally random extinctions; and (iii) assess the mechanisms explaining extra PD loss in these localities.

2. MATERIAL AND METHODS

We combined two comprehensive databases on mammal distributions [7] and phylogeny [6]. We considered 4796 terrestrial species for which we have data both on both phylogeny and geography. Excluded are recently described species with insufficient phylogenetic data; such species tend to capture little unique PD because they frequently represent recently elevated subspecies [6].

Threat status was obtained from the International Union for Conservation of Nature (<http://www.iucnredlist.org/>; see electronic supplementary material, table S1). A total of 1004 mammal species have been recognized as threatened (listed as vulnerable, endangered or critically endangered). Species with deficient data for evaluating threat status were considered unthreatened, although we are aware of suggestions that such species are likely to be threatened [14]. We defined PD loss as the difference between current PD and the remaining PD assuming the extinction of all threatened species (see electronic supplementary material, figure S1).

Distribution data were processed in ARCMAP v. 9.2, using 100 × 100 km grid cells on a Behrman equal area projection of the world. All analyses were performed in R (<http://www.r-project.org/>) with the APE package [17].

For each level of extinction intensity (11–60% extinct), we performed 1000 replicates, assigning extinction at random, to generate a null distribution of PD loss. In order to understand regional patterns, we additionally randomized extinction risk among species within each grid cell. The losses in (i) total PD, (ii) terminal branch length, and (iii) internal branch length were calculated for each simulation, respectively. If a cell's expected loss was higher than 95 per cent of the losses predicted from simulations, then this cell was considered at risk of significant higher loss than expected from random extinction.

3. RESULTS

The proportion of the mammalian tree of life that is lost through random extinction increases approximately linearly with extinction intensity ($r^2 = 0.997$;

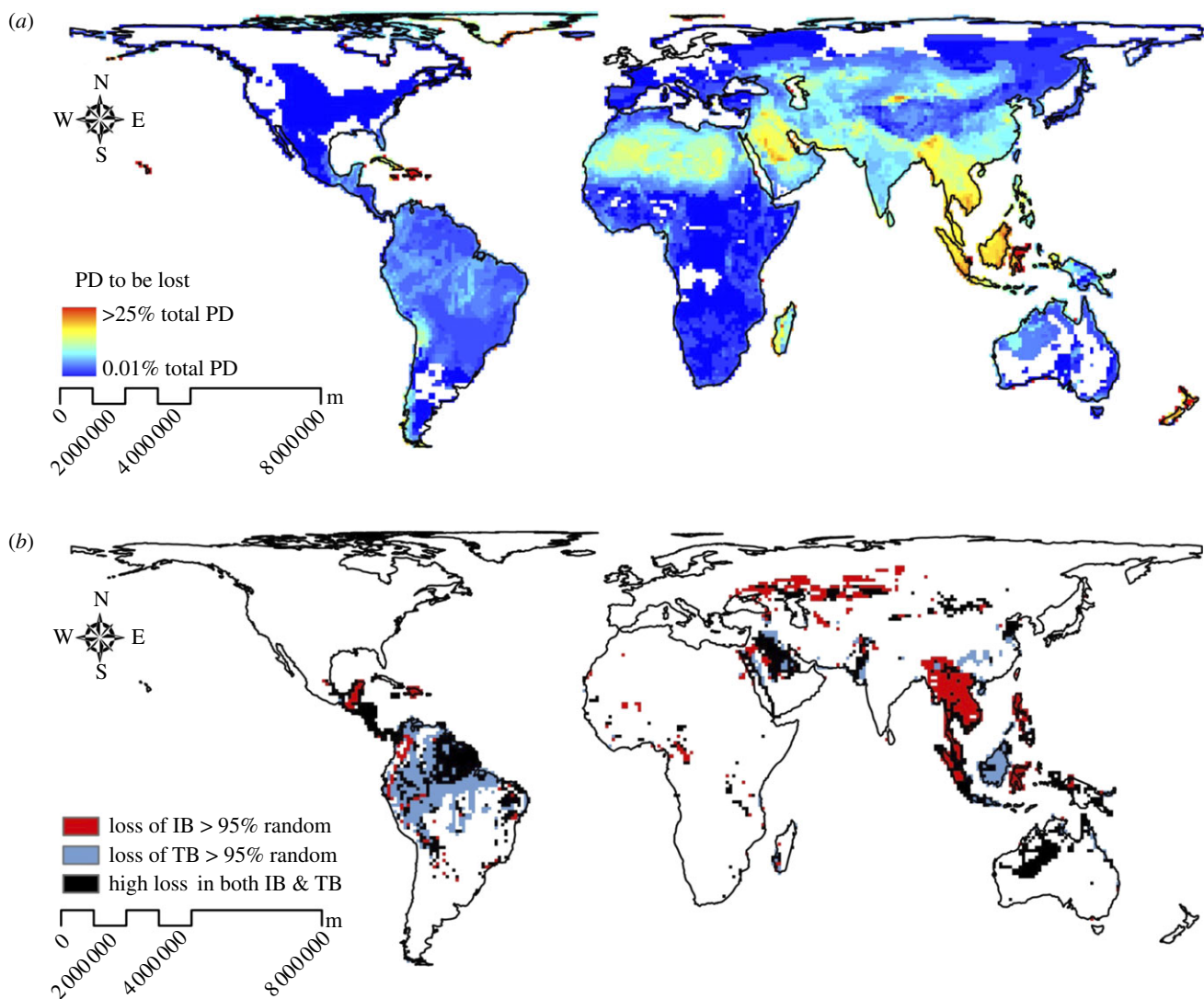


Figure 1. Predicted phylogenetic diversity (PD) to be lost with extinction of currently threatened species within each 100×100 km grid cell. The colours in (a) represent the percentage of PD to be lost, from low (blue) to high (red). The coloured areas in (b) indicate cells with risk of higher loss in PD than 95% random: higher loss in internal branch length (IB, red), higher loss in terminal branch length (TB, blue) and a combination of both (black).

electronic supplementary material, figure S2). Of current mammalian PD, 14 per cent would be lost if all currently threatened species become extinct. This result falls within the two-tailed 90 per cent interval (8151 Myr, 8961 Myr) from our null model of random extinction (electronic supplementary material, table S1).

Threatened mammals occur in approximately 76 per cent of global land areas and the intensity of threatened PD varies across space (figure 1a). Large areas in Southeast Asia and western Madagascar are at risk of losing a large proportion of PD, whereas the proportional loss in PD in the rest of Africa appears relatively low. Among cells harbouring threatened species, 22 per cent will lose greater PD than predicted by random extinction (figure 1b and electronic supplementary material, figure S1).

The high PD loss we observe in the Amazon and Borneo in Indonesia can be largely attributed to the loss of locally distinctive species (figure 1b and electronic supplementary material, figures S3 and S4); whereas local mammalian diversity in South Asian

and Mesoamerica, and the Ural–Caspian Steppes is threatened with the loss of many internal branches (figure 1b and electronic supplementary material, figures S3 and S5).

4. DISCUSSION

In contrast to the optimistic hypothesis that much of the tree of life might survive through a large extinction event [10], loss of mammal PD increases rapidly with extinction intensity. Over the complete mammal tree, the PD lost if currently threatened species become extinct is not significantly different from that predicted by chance. However, PD lost regionally varies strikingly across space. We used a null model of phylogenetically random extinction to search for areas where PD loss is higher than expected based simply on the number of threatened species. Estimated PD losses in most areas do not depart from random expectations; however, in some areas PD loss is much greater. For example, although the total amount of PD to be lost in the Amazon is not striking,

PD is lost at a greater rate than that expected from random extinctions. Global extinctions that result in little loss of global PD may therefore still have a large impact on ecosystems in some areas because they can result in a disproportionate loss of regional diversity. Critically, estimating global PD losses will tend to underestimate the impact of extinctions on regional biodiversity and may thus misinform conservation prioritizing actions.

The loss of PD reflects the number of threatened species plus the phylogenetic structure of extinction risk; here, we focus on explaining the latter. Large PD loss might result either because threatened species are evolutionarily distinct, or because they are clustered within clades so that close relatives share similar vulnerabilities. We show that the relative importance of these two mechanisms differs between regions. Higher-than-expected PD loss in the Amazon can be largely attributed to the loss of distinctive species. For example, in one Amazon cell (electronic supplementary material, figure S3), three of the nine threatened species are in the 5 per cent most evolutionarily distinct quantile of the local assemblage: Amazonian manatee *Trichechus inunguis* (with a terminal branch as long as 98.9 Myr), South American tapir *Tapirus terrestris* (85.3 Myr) and Pacarana *Dinomys branicki* (45.3 Myr; electronic supplementary material, figure S4). The Pacarana is also evolutionarily distinct globally (1% quantile). However, the manatee and tapir might not be considered globally distinctive (time to most recent common extant ancestor globally: 19.5 and 8.1 Myr for *Trichechus inunguis* and *Tapirus terrestris*, respectively), and therefore may be undervalued by global biodiversity metrics, such as EDGE [11]. Nonetheless, these species contribute substantially to regional biodiversity and should be considered as species of conservation importance. Other examples include the Asian wild ass *Equus hemionus* (endangered) in the Himalayas and the South American Tapir (vulnerable) in the Amazon, which have closely related species on the tree of life for mammals (less than 3 Myr apart), but are highly evolutionarily distinct within their local communities (over 80 Myr distant). Fine-scaled analyses are critical for identifying such species. By contrast, extinctions within South Asia and Mesoamerica would result in the loss of many internal branches, indicating that extinction is phylogenetically clumped. In one cell within the South Asian biodiversity hotspot (electronic supplementary material, figure S3), extinctions would result in the loss of seven of the eight primate species, removing several internal branches from the local ecosystem (electronic supplementary material, figure S5).

We have demonstrated that the impact of global-species extinctions on regional biodiversity strongly depends on geographical locality and the regional-species assemblage. Global analyses may underestimate impacts of extinction on ecosystem processes and function because they occur at finer spatial scales. Although extinction risk has been previously shown to demonstrate strong phylogenetic signal [16], we find that the phylogenetic distribution of risk varies considerably among regional mammal

assemblages. It is critical, therefore, that phylogenetic approaches to conservation are considered within a spatially explicit framework. Furthermore, although national Red Lists mostly concur with global Red Lists, species that are not recognized as globally threatened could potentially be lost at a regional scale [18]. Future data collection allowing assessments of potential PD loss from regional extinctions would probably amplify our results and vastly improve our estimates of the true impacts of species extinctions.

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