

# Species diversity as a surrogate for conservation of phylogenetic and functional diversity in terrestrial vertebrates across the Americas

Giovanni Rapacciuolo<sup>1,2,3\*</sup>, Catherine H. Graham<sup>3,4</sup>, Julie Marin<sup>5,6</sup>, Jocelyn E. Behm<sup>5</sup>, Gabriel C. Costa<sup>7</sup>, S. Blair Hedges<sup>5</sup>, Matthew R. Helmus<sup>5</sup>, Volker C. Radeloff<sup>8</sup>, Bruce E. Young<sup>2</sup> and Thomas M. Brooks<sup>9,10,11</sup>

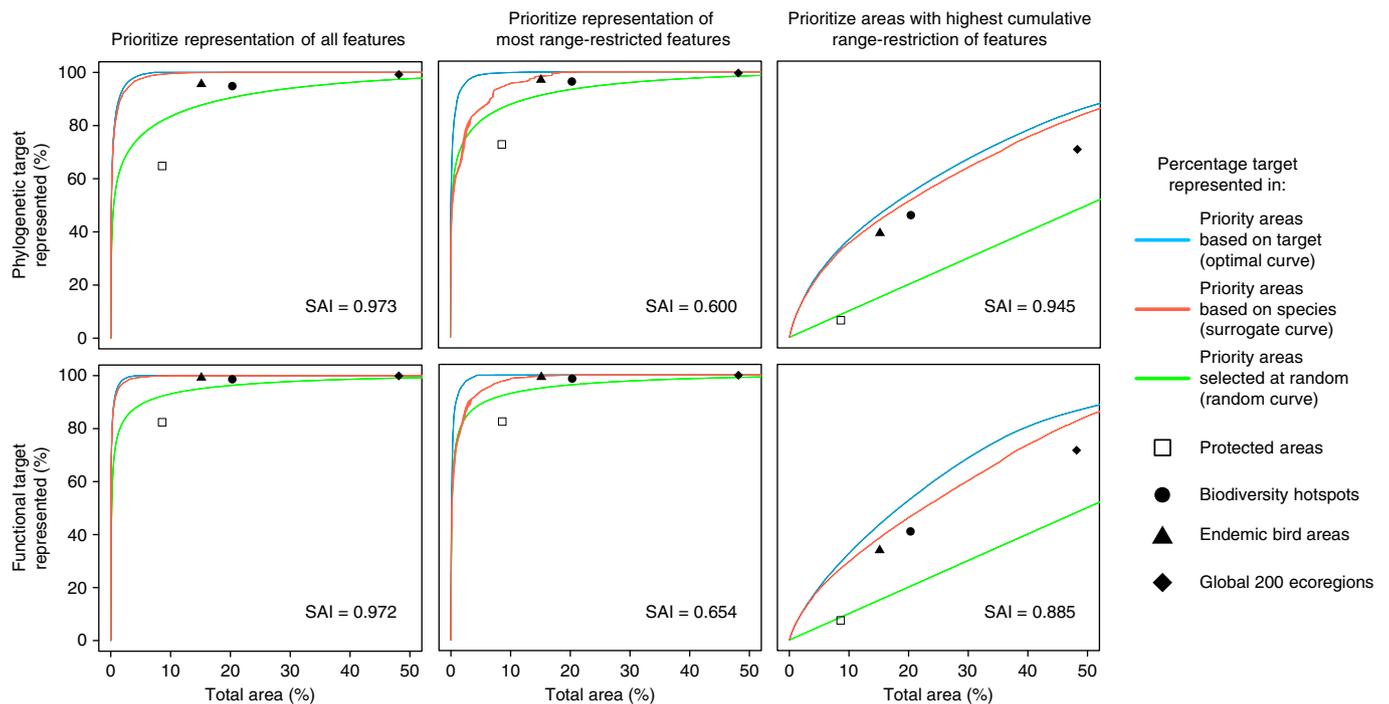
**Preserving the evolutionary history and ecological functions that different species embody, in addition to species themselves, is a growing concern for conservation. Recent studies warn that conservation priority regions identified using species diversity differ from those based on phylogenetic or functional diversity. However, spatial mismatches in conservation priority regions need not indicate low surrogacy among these dimensions in conservation planning. Here, we use data for 10,213 terrestrial vertebrate species across the Americas to evaluate surrogacy; that is, the proportion of phylogenetic or functional diversity represented in conservation plans targeting species. We find that most conservation plans targeting species diversity also represent phylogenetic and functional diversity well, despite spatial mismatches in the priority regions identified by each plan. However, not all phylogenetic and functional diversity is represented within species-based plans, with the highest-surrogacy conservation strategy depending on the proportion of land area included in plans. Our results indicate that targeting species diversity could be sufficient to preserve much of the phylogenetic and functional dimensions of biodiversity in terrestrial vertebrates of the Americas. Incorporating phylogenetic and functional data in broad-scale conservation planning may not always be necessary, especially when the cost of doing so is high.**

Humans are driving biodiversity loss at rates not experienced since the asteroid collision that ended the Cretaceous period 66 million years ago<sup>1</sup>. Contemporary biodiversity loss encompasses species extinctions (loss of species diversity<sup>2</sup>), pruning of the tree of life (loss of phylogenetic diversity<sup>3</sup>) and erosion of species' roles within ecosystems (loss of functional diversity<sup>4</sup>). Despite recent academic focus on phylogenetic and functional diversity<sup>5–8</sup>, limited conservation funds and inadequate data resources in practice limit most conservation plans to the use of species diversity as their target, under the assumption that it also adequately captures other dimensions of biodiversity. Recent studies have questioned this assumption of surrogacy by highlighting how maps of diversity<sup>9–12</sup> and outcomes from spatial conservation prioritization algorithms<sup>5–7,13</sup> show minimal overlap among dimensions of biodiversity. However, surrogacy is measured as the degree to which a given dimension is represented in conservation plans targeting another dimension and it technically cannot be assessed by comparing spatial correlations among different dimensions of biodiversity, as has been done in previous studies<sup>14–16</sup>. Therefore, applied conservation still needs robust evaluations of the extent to which species diversity serves as a surrogate for phylogenetic and functional diversity. If surrogacy is indeed low, much effort to incorporate data for the individual dimensions of biodiversity will be essential to plan and monitor progress towards conservation targets for species, phylogenetic and functional diversity. In contrast, if surrogacy is high,

conservation actions may proceed using species diversity as a target, secure in the knowledge that conserving species diversity also maintains most phylogenetic and functional diversity. As an additional consideration, assessments of surrogacy should also account for the nonrandom loss of phylogenetic<sup>3</sup> and functional diversity<sup>17</sup> that impending extinctions are expected to cause: surrogacy today may not necessarily persist in the future.

Here, we provide a quantitative test of the degree to which species diversity is a surrogate for phylogenetic and functional diversity in broad-scale conservation planning—now and in the future—using existing and newly compiled data on the distribution, phylogeny, ecological traits and extinction risk of 10,213 (~77%) species of tetrapod vertebrates across the Americas. Specifically, we quantified how well the diversity of phylogenetic and functional tree branches are represented in conservation plans established using species diversity across 110 km<sup>2</sup> equal-area grid cells. We then tested whether surrogacy is projected to change as a result of impending extinctions, by assuming that all species currently categorized as threatened on the International Union for Conservation of Nature (IUCN) Red List (vulnerable, endangered and critically endangered categories<sup>18</sup>) would go extinct. Finally, we asked how well current protected areas (<https://www.protectedplanet.net/>) and regions previously identified as important for the conservation of species diversity<sup>19–21</sup> represent phylogenetic and functional diversity. We obtained distribution and extinction risk data from the IUCN Red

<sup>1</sup>Life and Environmental Sciences, University of California Merced, Merced, CA, USA. <sup>2</sup>NatureServe, Arlington, VA, USA. <sup>3</sup>Department of Ecology and Evolution, Stony Brook University, New York, NY, USA. <sup>4</sup>Swiss Federal Institute for Forest, Snow and Landscape, Birmensdorf, Switzerland. <sup>5</sup>Center for Biodiversity, Department of Biology, Temple University, Philadelphia, PA, USA. <sup>6</sup>Institut de Systématique, Evolution, Biodiversité, UMR 7205, Département Systématique et Evolution, Muséum National d'Histoire Naturelle, Sorbonne-Universités, Paris, France. <sup>7</sup>Department of Biology, Auburn University at Montgomery, Montgomery, AL, USA. <sup>8</sup>SILVIS Lab, Department of Forestry and Wildlife Ecology, University of Wisconsin, Madison, WI, USA. <sup>9</sup>International Union for Conservation of Nature, Gland, Switzerland. <sup>10</sup>World Agroforestry Center, University of the Philippines Los Baños, Los Baños, Philippines. <sup>11</sup>Institute for Marine and Antarctic Studies, University of Tasmania, Hobart, Tasmania, Australia. \*e-mail: [giorapac@gmail.com](mailto:giorapac@gmail.com)



**Fig. 1 | Species diversity is a good surrogate for phylogenetic and functional diversity in conservation plans for terrestrial vertebrates of the Americas.** Performance of species diversity as a surrogate for phylogenetic (top) and functional diversity (bottom) based on three conservation strategies: 'Prioritize representation of all features' (left); 'Prioritize representation of most range-restricted features' (middle); and 'Prioritize areas with highest cumulative range-restriction of features' (right). The curves displayed represent the median and 95% CIs derived from the underlying sets of algorithm runs (10 for optimal and surrogate curves; 1,000 for random curves); note that CIs are very tight around the curves and are thus difficult to see. Also shown are the percentages of target biodiversity represented in regions considered important for conservation (protected areas, biodiversity hotspots, endemic bird areas and Global 200 ecoregions). Values displayed are median SAI values: a quantitative measure of surrogacy.

List<sup>18</sup>, phylogenetic data from TimeTree<sup>22</sup> and functional data from multiple sources, with body size the only trait available for >70% of all tetrapods of the Americas, but with diet, activity cycle, foraging height and reproductive mode also available for >70% of species in some classes (see Methods).

To evaluate surrogacy, we quantified how phylogenetic and functional diversity accumulate as additional grid cells are added to conservation plans (1) in the order that maximizes the rate of accumulation of phylogenetic or functional diversity directly (that is, the 'optimal' accumulation curve; see refs<sup>15,23</sup>), (2) in the order that maximizes the rate of accumulation of species diversity (that is, the 'surrogate' accumulation curve) and (3) based on 1,000 randomly generated grid cell sequences (that is, the 'random' accumulation curve). Because multiple iterations of the same conservation plan can lead to different spatial configurations and rates of accumulation of the target biodiversity<sup>15</sup>, we obtained estimates of variation around the optimal and surrogate accumulation curves by running each conservation plan ten times. We then used these three sets of biodiversity accumulation curves to generate species accumulation indices (SAIs) of surrogacy<sup>15,23</sup>. The SAI is calculated as  $(s - r) / (o - r)$ , where  $s$ ,  $r$  and  $o$  are the areas under the surrogate, random and optimal curves, respectively<sup>15,23</sup>. The SAI equals 1 when the optimal and surrogate curves are identical (perfect surrogacy), between 1 and 0 when the surrogate curve lies above the random curve (positive surrogacy), 0 when the surrogate and random curves coincide (no surrogacy) and <0 when the surrogate curve lies below the random curve (negative surrogacy). Finally, to explore the influence of the specific conservation strategy on surrogacy, we established conservation plans using three different spatial conservation prioritization algorithms. Each algorithm selects areas in the order that prioritizes different aspects of the diversity of target features (phylogenetic

branches, functional branches or species): the first prioritizes the representation of all features, with all features treated equally; the second prioritizes the representation of the most range-restricted features; and the third prioritizes areas with the highest cumulative range-restriction across features (Supplementary Table 1).

## Results and discussion

**Surrogacy value of species diversity for conserving phylogenetic and functional diversity.** Species diversity is a good surrogate for conserving both the phylogenetic and functional diversity of tetrapod vertebrates across the Americas (Fig. 1 and Tables 1 and 2). Median surrogacy values for phylogenetic and functional diversity are  $\geq 0.89$  for the 'Prioritize representation of all features' and 'Prioritize areas with highest cumulative range-restriction of features' conservation plans, and  $\geq 0.6$  for the 'Prioritize representation of most range-restricted features' conservation plan across all taxa. These surrogacy values indicate that targeting species diversity is, on average,  $\geq 60\%$  as effective at representing aspects of phylogenetic and functional diversity compared with conservation plans targeting phylogenetic or functional diversity directly. Although conservation plans targeting functional diversity across all tetrapods (Fig. 1 and Table 1) are based on a simplified tetrapod-level functional space reflecting variation in body mass only, high surrogacy is maintained even when we use more complex multivariate functional spaces for each tetrapod class individually (Table 2 and Supplementary Figs. 2–5; see Methods). Indeed, mammals, which show the lowest surrogacy of all tetrapod classes between species and functional diversity, still display surrogacy values of  $\geq 0.70$ , while amphibians display the highest surrogacy values on average ( $\geq 0.89$ ; Table 2). Additionally, we find that surrogacy values are largely consistent among different iterations of each conservation plan, as exemplified by the tight 95%

confidence intervals (CIs) around median surrogacy curves (Fig. 1 and Supplementary Figs. 2–5) and values (Tables 1 and 2).

The degree of surrogacy varies with the conservation strategy and the percentage of land area included in conservation plans. The surrogacy value of species diversity is lowest for the ‘Prioritize representation of most range-restricted features’ conservation plan, which even exhibits negative SAI values for both phylogenetic and functional diversity across the top 4% priority areas (Figs. 1 and 2). Indeed, specifically targeting the most range-restricted species misses most widespread species initially (up to about 20% of land area; see Supplementary Fig. 6) and, consequently, the proportion of phylogenetic and functional variation represented by these species. This is particularly the case at the tetrapod level, where functional variation is represented exclusively by body mass; given the strong positive correlation between body mass and range size<sup>24</sup>, prioritizing range-restricted species will fail to represent many large-bodied species within high-priority areas. Nevertheless, SAI values for the ‘Prioritize representation of most range-restricted features’ conservation plan remain lower than other plans, even for more complex functional spaces, indicating that this pattern is not driven uniquely by body mass.

Surrogacy increases rapidly with the proportion of land area included in the ‘Prioritize representation of all features’ and ‘Prioritize representation of most range-restricted features’ conservation plans, both of which maximize the rate of accumulation of all biodiversity target features across the Americas. In contrast, when using the ‘Prioritize areas with highest cumulative range-restriction across features’ strategy, surrogacy is high for low proportions of area but declines as more areas are added, before increasing again towards a value of 1. This pattern stems from this plan’s focus on including important areas—regardless of the features they encompass—rather than including all features (see Supplementary Table 1). Thus, while this plan initially leads to the inclusion of areas with high diversity across all three biodiversity dimensions, the features included in additional areas eventually become redundant with those of previously included areas, such that the overall surrogacy of priority areas declines until all land area and features eventually become represented in the plan.

Convention on Biological Diversity Aichi Target 11 recommends conserving 17% of global land area. Under this target, species diversity is a very good surrogate for phylogenetic and functional diversity at the tetrapod level (that is, surrogacy of  $\geq 0.80$ ), across all 3 conservation strategies (Fig. 2).

Surrogacy between species and both phylogenetic and functional diversity at the tetrapod level is projected to remain high in the face of impending extinctions for most conservation plans (Table 1). Regardless of how uncertainty in species extinctions is handled (that is, all data-deficient species coded as ‘least concern’ versus all coded as threatened; see Methods), most conservation plans targeting species diversity have projected surrogacy values comparable to current values (Table 1). Therefore, prioritizing areas identified as important for species now is likely to increase future persistence for all three dimensions of biodiversity. There is one exception: conservation plans maximizing the rate of accumulation of the rarest species using the ‘Prioritize representation of most range-restricted features’ strategy are unlikely to represent the rarest functional (that is, body mass) classes very well in the face of impending extinctions, particularly if we assume that all data-deficient species are threatened (Table 1). This makes sense considering that body mass and range restriction are both strong predictors of extinction risk across terrestrial vertebrates<sup>17,25–27</sup>; therefore, drastically reducing variation in both body mass and rarity via the exclusion of threatened and data-deficient species may decouple species rarity from body mass variation in the remaining set of species, thereby reducing surrogacy between species and functional diversity.

Our finding of good species surrogacy appears to differ from previous studies emphasizing mismatches among regions of high

**Table 1 | The value of species diversity as a surrogate for conserving phylogenetic and functional diversity in tetrapods across the Americas, now and in the projected future**

Conservation plan	Surrogacy value of species diversity	
	Phylogenetic target	Functional target
<b>Prioritize representation of all features</b>		
Current (all risk categories)	0.97 (0.97, 0.98)	0.97 (0.97, 0.98)
Projected (DD not threatened)	0.97 (0.96, 0.97)	0.97 (0.96, 0.97)
Projected (DD threatened)	0.96 (0.95, 0.97)	0.96 (0.95, 0.97)
<b>Prioritize representation of most range-restricted features</b>		
Current (all risk categories)	0.60 (0.50, 0.67)	0.65 (0.57, 0.71)
Projected (DD not threatened)	0.58 (0.49, 0.66)	0.53 (0.43, 0.61)
Projected (DD threatened)	0.61 (0.48, 0.70)	0.22 (–0.01, 0.38)
<b>Prioritize areas with highest cumulative range-restriction of features</b>		
Current (all risk categories)	0.94 (0.94, 0.95)	0.89 (0.88, 0.89)
Projected (DD not threatened)	0.96 (0.96, 0.96)	0.88 (0.87, 0.88)
Projected (DD threatened)	0.97 (0.97, 0.97)	0.87 (0.86, 0.87)

Median SAI values are shown, with 95% CIs in parentheses. An SAI value of 1.00 would indicate that 100% of phylogenetic or functional branches are represented within species-based priorities. DD, species categorized as data deficient in the IUCN Red List.

diversity<sup>9–12</sup> or conservation priority<sup>5–7,13</sup> identified using each dimension of biodiversity individually. However, these mismatch comparisons do not technically test for surrogacy because they do not quantify how plans established using alternative dimensions (specifically, species diversity) represent target dimensions. Replicating the methods of these previous studies, our results concur with their findings: maps of commonly used biodiversity metrics reveal large mismatches among species, phylogenetic and functional dimensions for tetrapod vertebrates of the Americas (Supplementary Fig. 6a and Supplementary Table 4). Similarly, spatial conservation prioritizations generated using commonly used software such as Zonation<sup>28</sup> (Supplementary Fig. 6b) show substantial spatial mismatch and are weakly correlated among dimensions of biodiversity (Supplementary Table 5). Yet, we find that spatial prioritizations based on species (Supplementary Fig. 6b) represent phylogenetic and functional diversity per unit area to an extent comparable to that of spatial prioritizations identified using phylogenetic and functional diversity directly (Supplementary Fig. 6c). As a result, comparisons between conservation prioritizations based on single dimensions (species, phylogenetic and functional) can reveal low spatial overlap even while tests of the representation of phylogenetic or functional diversity in a conservation plan based on species reveal high surrogacy<sup>29</sup>. An explanation for these differences is that analyses of spatial overlap are highly sensitive to the exact priority rankings of areas derived from each individual dimension, because they assess agreement among dimensions using correlations either among the full sets of rankings (for example, ref. <sup>6</sup>) or among areas above a certain rank (for example, refs <sup>5,6</sup>). In contrast, surrogacy tests assess the potential of a whole network of areas to adequately represent different dimensions: they do not consider the priority ranking of areas, but instead test how adequate an entire set of areas is at representing each biodiversity dimension.

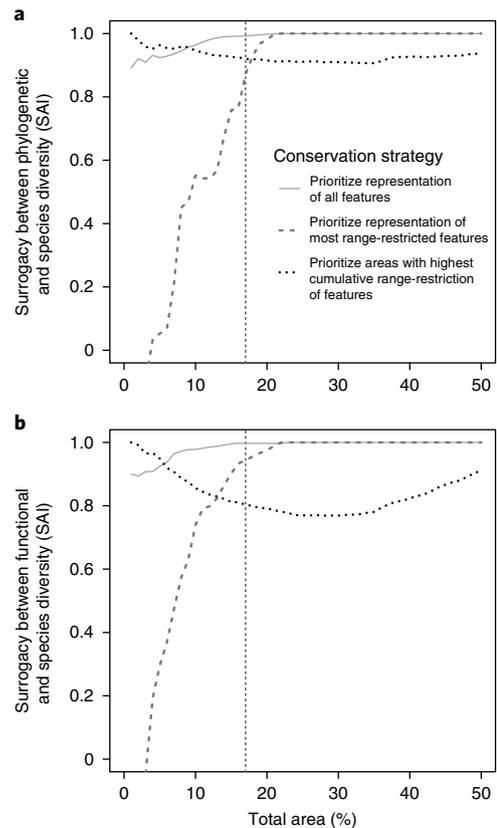
**Species-based conservation plans do not represent all phylogenetic and functional diversity.** Our results also show that conservation plans targeting species diversity do not represent all

**Table 2 | The value of species diversity as a surrogate for conserving phylogenetic and functional diversity for individual tetrapod classes across the Americas**

Conservation plan	Surrogacy value of species diversity	
	Phylogenetic target	Functional target
<b>Amphibians</b>		
Prioritize representation of all features	0.98 (0.98, 0.99)	0.98 (0.98, 0.98)
Prioritize representation of most range-restricted features	0.77 (0.71, 0.91)	0.89 (0.87, 0.91)
Prioritize areas with highest cumulative range-restriction of features	0.95 (0.95, 0.78)	0.95 (0.94, 0.95)
<b>Birds</b>		
Prioritize representation of all features	0.99 (0.98, 1.00)	0.99 (0.98, 0.99)
Prioritize representation of most range-restricted features	0.70 (0.55, 2.15)	0.73 (0.60, 0.80)
Prioritize areas with highest cumulative range-restriction of features	0.92 (0.92, 0.80)	0.93 (0.92, 0.93)
<b>Mammals</b>		
Prioritize representation of all features	0.95 (0.94, 0.91)	0.95 (0.93, 0.96)
Prioritize representation of most range-restricted features	0.66 (0.54, 0.57)	0.70 (0.60, 0.76)
Prioritize areas with highest cumulative range-restriction of features	0.90 (0.90, 0.82)	0.93 (0.92, 0.93)
<b>Reptiles</b>		
Prioritize representation of all features	0.97 (0.96, 0.97)	0.96 (0.96, 0.97)
Prioritize representation of most range-restricted features	0.68 (0.59, 0.39)	0.71 (0.63, 0.76)
Prioritize areas with highest cumulative range-restriction of features	0.92 (0.91, 0.68)	0.93 (0.93, 0.90)

Median SAI values are shown, with 95% CIs in parentheses. An SAI value of 1.00 would indicate that 100% of phylogenetic or functional branches are represented within species-based priorities.

phylogenetic and functional diversity. To gain a better understanding of the degree of phylogenetic and functional diversity not represented within plans targeting species diversity, we quantified the total phylogenetic and functional distinctiveness (measured using the fair proportion method<sup>30</sup>) not included in species-based priority areas (Fig. 3). We find that the total phylogenetic and functional distinctiveness of species not included in species-based priority areas is relatively high across the top 10% priority areas but drops sharply as additional areas are added to conservation plans. This decay is slowest for the ‘Prioritize representation of most range-restricted features’ strategy. As mentioned above, this plan’s focus on prioritizing range-restricted species causes it to initially miss the proportion of phylogenetic and functional variation associated with widespread species. Although many evolutionarily and functionally unique species are range-restricted<sup>31</sup>, the converse is not necessarily true: evolutionarily and functionally unique species can also be widespread<sup>32</sup>, while many range-restricted species are neither evolutionarily nor functionally unique<sup>33</sup> (for example, recently split or cryptic species).

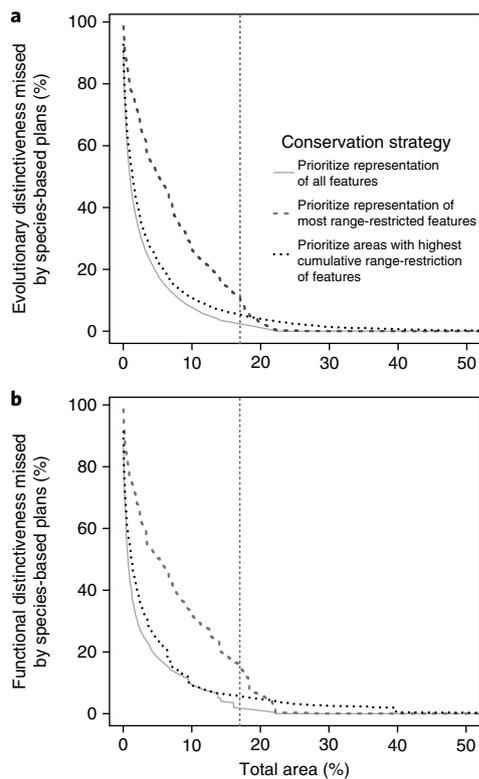


**Fig. 2 | Value of species diversity as a surrogate for phylogenetic and functional diversity.** **a, b**, SAI values of surrogacy for phylogenetic (**a**) and functional diversity (**b**) in terrestrial vertebrates for each 1% increment of land area across the Americas. Lines represent the various conservation strategies, as defined by the legend. The dashed, vertical line indicates 17% of land area—the global coverage target included in Convention on Biological Diversity Aichi Target 11.

Under the 17% land area target, the ‘Prioritize representation of all features’ and ‘Prioritize areas with highest cumulative range-restriction of features’ conservation plans fail to represent up to 5% of phylogenetic distinctiveness and up to 6% of functional distinctiveness across the Americas. Under this same land area target, ‘Prioritize representation of most range-restricted features’ conservation plans fail to represent up to 10% of phylogenetic (13,038 million years) and up to 15% of functional distinctiveness (functional tree branch units are not meaningful). It is important to note that these estimates represent the ‘worst-case’ scenarios (that is, the highest total distinctiveness values among the ten iterations we ran for each conservation plan).

Overall, our results suggest that conservation plans either targeting all species—regardless of their degree of range restriction—or targeting areas with the highest cumulative range-restriction of species will ensure the best representation of both phylogenetic and functional diversity across a small network of areas. However, conservation plans prioritizing the representation of the most range-restricted species are a better option than those prioritizing areas with the highest cumulative range-restriction of species across larger networks of areas (that is, including 20% or more of available land area).

**Surrogacy value of areas of conservation importance.** Protected areas represent less biodiversity than if they were chosen randomly;



**Fig. 3 | Proportion of evolutionary and functional distinctiveness not represented within species-based conservation plans. a, b.** The curves summarize the total evolutionary (a) and functional distinctiveness (b) values of species missed from species-based conservation plans (the maximum value across 10 iterations) for each 1% increment of land area across the Americas. The dashed vertical line indicates 17% of land area—the global coverage target included in Convention on Biological Diversity Aichi Target 11.

the current distribution of protected areas displays very low or negative surrogacy for both phylogenetic and functional diversity (Table 3 and Fig. 1). In contrast, biodiversity hotspots<sup>19</sup> and other globally recognized regions of conservation importance originally defined using aspects of species diversity (that is, endemic bird areas<sup>20</sup> and Global 200 ecoregions<sup>21</sup>) display good surrogacy for phylogenetic diversity and excellent surrogacy for functional diversity across the Americas (Table 3, Fig. 1 and Supplementary Figs. 2–5). These surrogacy estimates are based on the set of grid cells with at least 50% of land area overlapped by important conservation areas, but surrogacy values were robust across different land area thresholds (Supplementary Table 6). These results corroborate recent findings and suggest that protected area delineation, which is often the result of political opportunism, may represent biodiversity poorly in many cases, especially when compared with biologically motivated areas of conservation importance<sup>34</sup>.

**Outlook.** Our findings indicate that conservation areas selected based on species diversity will also represent most, but not all, phylogenetic and functional diversity. Generalization of these findings comes with three main caveats. First, although the 110km<sup>2</sup> grid cell resolution of our study, and targets such as the conservation of 17% of land area, are consistent with the spatial scale used in broad-scale conservation plans (for example, the allocation of globally flexible resources<sup>35</sup>), site-level conservation actions and protected area delineation will take place at finer scales. In-depth assessments of surrogacy and confirmation of our findings at such finer scales

**Table 3 | The value of broad-scale conservation priority regions for conserving the phylogenetic and functional diversity of tetrapods across the Americas**

Broad-scale conservation priorities	Surrogacy value	
	Phylogenetic target	Functional target
<b>Protected areas</b>		
Prioritize representation of all features	−0.98 (−1.51, −0.59)	−1.32 (−1.99, −0.87)
Prioritize representation of most range-restricted features	−1.75 (−3.52, −0.92)	−1.86 (−3.10, −1.08)
Prioritize areas with highest cumulative range-restriction of features	−0.09 (−0.15, −0.04)	−0.07 (−0.13, −0.01)
<b>Endemic bird areas</b>		
Prioritize representation of all features	0.64 (0.54, 0.72)	0.84 (0.79, 0.87)
Prioritize representation of most range-restricted features	0.80 (0.72, 0.86)	0.91 (0.88, 0.93)
Prioritize areas with highest cumulative range-restriction of features	0.83 (0.82, 0.84)	0.80 (0.78, 0.81)
<b>Biodiversity hotspots</b>		
Prioritize representation of all features	0.49 (0.33, 0.60)	0.75 (0.67, 0.81)
Prioritize representation of most range-restricted features	0.51 (0.33, 0.64)	0.76 (0.68, 0.82)
Prioritize areas with highest cumulative range-restriction of features	0.82 (0.81, 0.83)	0.78 (0.77, 0.80)
<b>Global 200 ecoregions</b>		
Prioritize representation of all features	0.68 (0.54, 0.78)	0.89 (0.84, 0.92)
Prioritize representation of most range-restricted features	0.71 (0.56, 0.80)	0.89 (0.83, 0.93)
Prioritize areas with highest cumulative range-restriction of features	0.65 (0.62, 0.67)	0.68 (0.66, 0.69)

Median SAI values are shown, with 95% CIs in parentheses. An SAI value of 1.00 would indicate that 100% of phylogenetic or functional branches are represented within conservation priority regions. Negative SAI values indicate conservation priority regions that represent phylogenetic or functional branches less well than randomly selected areas.

will necessitate fine-scale biodiversity data, which are becoming increasingly available, for instance, through the identification of key biodiversity areas<sup>36</sup>. Second, our conclusion that species diversity is a good surrogate for functional diversity at the tetrapod level is based exclusively on variation in body mass. Although body mass is undoubtedly a fundamental axis of functional variation in tetrapods, it remains to be seen whether tetrapod-level surrogacy remains high for more complex functional spaces. Our results for individual tetrapod classes (especially for birds and mammals, for which we can incorporate four different traits in calculating functional diversity) indicate that this may be the case. Finally, it remains unclear whether species represent a good surrogate for phylogenetic and functional diversity in different regions (given that the Eastern Hemisphere differs from the Western Hemisphere in its underlying biogeography<sup>37</sup> and human pressure history<sup>38</sup>) or different species groups (given that results for tetrapods are not necessarily representative of all biodiversity<sup>39</sup>).

Nevertheless, these findings have important applied implications for conservation. Species data are much more comprehensive and cheaper to obtain than phylogenetic or functional data, and this is unlikely to change in the foreseeable future<sup>40</sup>. If species diversity were a poor surrogate for phylogenetic or functional diversity, a case could be made that conservation plans should be delayed to allow incorporation of such evolutionary and ecological datasets. Our findings suggest that such a delay may be unnecessary when the cost of waiting is high: broad-scale conservation planning can focus on optimizing the representation of species, with confidence that these plans represent other dimensions of biodiversity as well. Moreover, this high surrogacy is likely to persist into the future. Given the current high rate of biodiversity loss and ensuing urgency of action for conservation, this confidence is welcome.

## Methods

**Species dimension.** We obtained polygon range maps for all extant species of terrestrial tetrapod vertebrates native to the Americas: 3,344 amphibians<sup>18</sup>, 4,273 birds<sup>41</sup>, 1,751 mammals<sup>18</sup> and 3,491 non-avian reptiles<sup>18</sup> (hereafter, simply 'reptiles'; including squamates, freshwater turtles and crocodylians). Squamate maps for the Caribbean and Central and South America are the result of a recent effort by NatureServe and IUCN to assess the distribution and extinction risk of reptile species in those regions (for example, ref. <sup>42</sup>). Distribution and extinction risk data for squamate species of South America and the Caribbean are currently being processed by IUCN and will be provided shortly in a format akin to that used for other taxa (via ref. <sup>18</sup>). We extracted range maps onto a Behrmann equal-area grid with a resolution of 110 km<sup>2</sup> (approximately 1° at the equator) at the Americas extent. We excluded all grid cells with less than 20% of land cover from our analyses.

**Phylogenetic dimension.** We obtained phylogenetic information across tetrapods from the TimeTree of Life—a compilation of 2,274 studies representing 50,632 species<sup>43</sup>. From this overall tree, we generated a smoothed time tree composed of six clades (amphibians, birds, crocodylians, mammals, squamate reptiles and turtles), including as many of our study species as possible. We interpolated species without any genetic data if at least one member of their genus had genetic information<sup>22,43</sup>. We considered 'reptiles' as a single taxon in our analyses, by combining data for squamate reptiles, crocodylians and turtles.

To represent the phylogenetic dimension in our spatial prioritization analyses based on this phylogeny, we used the phylogeny's branches as our target features to be conserved across the landscape. We followed the approach of recent authors<sup>5,8,13</sup>, in turn adapted from Rodrigues and Gaston<sup>44</sup>. First, we constructed a species-by-node matrix, where each node was assigned a binary presence for each species ancestrally derived from it and an absence for each species not derived from it. For instance, all species were assigned a presence for the most ancestral node. We then derived a cell-by-node matrix by multiplying the species-by-node matrix by the cell-by-species distribution matrix. We generated maps of each node and used those as the phylogenetic features to be targeted for conservation prioritization. We repeated this procedure for each tetrapod class separately and for all tetrapod species combined.

**Functional dimension.** We obtained species-level trait data for amphibians, reptiles, birds and mammals of the Americas from the most recent global compilations<sup>15–30</sup>. The four tetrapod classes differed in the type and completeness of available trait data. To maximize the amount of information included in the functional dimension of each taxon, we selected alternative trait datasets for each separate study taxon (amphibians, reptiles, birds, mammals and tetrapods overall). For each taxon, we selected all traits with complete information for 70% or more of the study species. At the tetrapod level, this approach resulted in the selection of a single trait:  $\log_{10}[\text{body mass}]$ . Although body size variation captures multiple aspects of a species' niche and function<sup>51</sup>, it may not reflect the more complex functional space that could be defined by a range of traits, and our tetrapod-level results should be interpreted with this in mind. At the level of individual classes, however, we were able to explore more complex functional spaces. For mammals and birds, we included available data on body mass, diet, activity cycle and foraging height<sup>45</sup>. These data have recently been used in similar analyses<sup>57</sup>. For amphibians and reptiles, we were able to include one additional trait alongside body mass: foraging height for amphibians<sup>49</sup> and reproductive mode for reptiles<sup>46</sup>. Body mass values for a subset of bird, mammal and reptile species (combined, equal to 4% of all tetrapod species) were imputed based on genus-level body mass means<sup>39,41</sup>. This could theoretically increase the correlation between functional and phylogenetic diversity for these taxa and tetrapods overall. However, we found no difference in the phylogenetic signal of body mass in birds, mammals and reptiles with or without imputed species (Supplementary Table 2). Given this negligible effect on phylogenetic signal, and the benefit of a more inclusive sample of tetrapods of the Americas, we included the 4% of genus-imputed tetrapod species within functional analyses and have no reason to believe that this affected

our findings. Additionally, it should be noted that the body mass values we used for reptiles represent maximum body mass estimates<sup>47</sup>, unlike the values used for amphibians, birds and mammals, which are mean body mass values; however, when combined at the tetrapod level, these data provide reliable estimates of relative differences in tetrapod-level body mass variation—a proxy for functional diversity—among cells<sup>50</sup>.

To represent the functional dimension in our spatial prioritization analyses, we generated functional trait trees (that is, dendrograms), using the relevant set of traits for each taxon, and subsequently reproduced all steps undertaken for the phylogenetic tree-based spatial prioritization analyses. For tetrapod-level functional trees, we calculated Euclidean distances between body mass values for each pair of species. For the analyses of each individual tetrapod class, we calculated Gower dissimilarity values for each species pair, based on the relevant combination of continuous, binary and categorical traits. We then used each distance/dissimilarity matrix within an unweighted pair group method with arithmetic mean clustering analysis to generate the trait dendrograms on which to base conservation plans.

**Extinction risk.** The IUCN Red List of Threatened Species<sup>48</sup> (hereafter, 'Red List') documents categorical extinction risks for all species of tetrapod vertebrates in this study, towards which we coordinated the assessments for Caribbean and Central and South American squamate species as described above. The Red List is based on the application of four quantitative criteria based on symptoms of elevated extinction risk (criteria A–D) with a criterion E based on comprehensively quantitative calculation of extinction risk through population viability analysis or similar approaches<sup>52,53</sup>. Quantitative thresholds for each of these criteria determine categories of extinction risk for three categories within which species have, at a minimum, a high risk of extinction in the wild in the medium-term future<sup>52,53</sup> (in order of increasing risk): vulnerable; endangered; and critically endangered. Species in these three categories are collectively considered 'threatened'.

Species for which insufficient information exists to undertake a Red List assessment are categorized as data deficient. Species that have already become extinct are categorized as extinct or extinct in the wild, as appropriate. Non-threatened species are assessed as near threatened (if parameters are documented to approach the thresholds for vulnerable) or least concern.

**Combined dataset.** After integrating data on the species, phylogenetic and functional dimensions of biodiversity, together with extinction risk, we were able to analyse 10,213 species of tetrapods across the Americas. This dataset represents approximately 77% of species and 88% of families of tetrapods documented in the Americas, including 2,476 amphibian species, 3,828 bird species, 1,582 mammal species and 2,351 (non-avian) reptile species (2,257 squamates, 71 freshwater turtles and 23 crocodylians). The missing ~23% of species could not be included in the dataset because they were missing phylogenetic information, had insufficient trait information or were not assessed for extinction risk. An overview of the species and families missing from our analysis is presented in Supplementary Fig. 1 and Supplementary Table 3. Given the high proportion of both tetrapod species and families included in our analysis, as well as the taxonomic distribution of missing species, we believe that the results we present in this paper are representative for tetrapods of the Americas overall.

**Phylogenetic and functional diversity metrics.** The approach of comparing the spatial configuration of hotspots among biodiversity dimensions (see Fig. 3) has previously been used to assess the surrogacy among biodiversity dimensions in a conservation context. We reproduced these analyses by calculating a range of measures of phylogenetic and functional diversity commonly used in studies comparing spatial patterns among dimensions of biodiversity with a conservation planning focus (for example, refs <sup>9–12,54–56</sup>). We quantified phylogenetic and functional diversity, respectively, from the phylogenetic trees and functional trait trees for each taxon, using mean pairwise distance<sup>57</sup> and Faith's phylogenetic diversity<sup>58</sup>. We calculated all phylogenetic and functional metrics using the R package PEZ<sup>59</sup> and estimated correlations among metrics using Tjostheim's coefficient—a variant of the correlation coefficient that takes into account the spatial context of the two variables.

**Regions of conservation importance.** We obtained data on protected areas (<https://www.protectedplanet.net/>), biodiversity hotspots<sup>19</sup>, endemic bird areas<sup>20</sup> and Global 200 ecoregions<sup>21</sup> from a previous compilation<sup>35</sup>. Spatial polygon layers for these four types of conservation regions have different spatial resolutions from each other and from the resolution of our study. As a result, aggregating them to our 110 km<sup>2</sup> equal-area grid over the Americas required setting a minimum threshold percentage of land cover to determine whether a given grid cell—and the biodiversity within it—was included or excluded within each conservation region. Throughout the paper, we display results for a 50% threshold: a given grid cell and its associated biodiversity were included within a conservation region if at least 50% of that grid cell was overlapped by that conservation region's polygons. We assessed the sensitivity of our results to this choice of threshold by re-running the corresponding analyses across a range of thresholds, and found that the results were largely consistent across thresholds (see Supplementary Table 6).

**Conservation strategies.** For each set of biodiversity target features (species, phylogenetic or trait branches), we generated conservation plans using three alternative conservation strategies, each of which was applied using a different spatial prioritization algorithm.

The 'Prioritize representation of all features' strategy was applied using a 'greedy' selection algorithm<sup>23,60</sup> implemented in R, using the approach developed by Ferrier<sup>23</sup> and code modified from Sabatini et al.<sup>61</sup>. The greedy algorithm selects grid cells in the order that maximizes the rate of accumulation of all features in the study area. It does so by assuming that a single occurrence of a feature within a cell is sufficient for that feature to be fully represented within a conservation plan and by weighting all targets equally. In practice, the greedy algorithm first prioritizes the cell (or one of the set of cells) including the highest proportion of all features in the study area, then prioritizes the cell with the highest proportion of all features in the study area not already represented in the previous cell, and so forth, until all biodiversity features in the study area are represented.

The 'Prioritize representation of most range-restricted features' strategy was applied using the core-area zonation algorithm implemented within the spatial conservation planning software Zonation<sup>28</sup> and run via the R package zonator<sup>62</sup>. The core-area zonation algorithm takes into account the proportion of the study area-wide range size of each biodiversity feature included in each grid cell and prioritizes grid cells in an order that maximizes the rate of accumulation of the single feature with the smallest range size (that is, most range restricted) first, and that with the largest range size last (hence, features are prioritized by their range size). In practice, the core-area zonation algorithm first prioritizes the cell (or one of the set of cells) that includes the highest proportion of any single feature (for example, single-cell endemic), then prioritizes the next remaining cell that includes the highest proportion of any single feature, and so forth, until all biodiversity features are represented.

The 'Prioritize areas with highest cumulative range-restriction across features' strategy was applied using the additive benefit function algorithm, also implemented in Zonation<sup>28</sup>. Similarly to core-area zonation, the additive benefit function algorithm also accounts for the range size of features within the study area, but it uses this information differently: it sums the proportion of each feature's range size contained in a given cell across all features included in the cell, and prioritizes the grid cells with the highest summed proportions (that is, the areas with the highest number of range-restricted features). Therefore, the additive benefit function gives more importance than core-area zonation to the number (that is, more features = a higher summed proportion) of features within cells, potentially at the expense of the most range-restricted features over the entire study area (see Supplementary Table 1).

In addition, for Zonation runs using both the core-area zonation and additive benefit function algorithms, we included phylogenetic or functional tree branch lengths as weights for each corresponding phylogenetic or functional feature across the study area, such that deeper branches were given a higher priority than shallower branches within these conservation plans.

Although the spatial prioritization algorithms we used were originally designed to use species as target features, this is not a strict requirement. All three algorithms simply require a set of spatial features (whose diversity we wish to maximize) and their distribution across a finite landscape. In addition, for all but the greedy algorithm, spatial features can also be weighted by some variable, with higher weights being given higher priority within plans. Consequently, a number of recent studies have used several of these algorithms to target phylogenetic and/or functional features such as branches or classes<sup>5–7</sup>. Here, we used each of the three conservation strategies to prioritize not only species but also the spatial distribution of phylogenetic and functional branches. Our Zonation-based analyses follow a very similar protocol to Pollock et al.<sup>5</sup>, with our 'Prioritize representation of all features' and 'Prioritize areas with highest cumulative range-restriction across features' strategies corresponding to the 'maximize global diversity' and 'maximize local diversity' strategies in ref. <sup>5</sup>. We ran spatial prioritizations for tetrapods overall, and for each tetrapod class individually.

Complementary representation problems such as spatial prioritizations for conservation will often have multiple solutions, such that different runs of the same algorithm–target combination may generate different maps of spatial prioritizations<sup>15</sup>. As a result, we ran ten iterations of each algorithm–target combination. Across all taxa, we found that ten iterations were sufficient to capture most of the variation in the rate of accumulation of the target biodiversity among individual algorithm runs, as exemplified by the tight confidence intervals (CIs) around the accumulation curves and surrogacy values we report (see Fig. 1 and Tables 1 and 2).

**Surrogacy measure.** In assessing the degree to which conserving species serves as a surrogate for evolutionary history and functional diversity, we calculated an SAI<sup>15,23,60</sup>. The SAI is derived from the comparison of three curves documenting the increase in 'target' biodiversity (in our case, either phylogenetic or functional diversity) as different areas are prioritized for conservation, using three approaches: optimal; using a 'surrogate' (in our case, species diversity); or random.

First, the 'optimal curve' represents the accumulation of the target biodiversity (that is, phylogenetic or functional diversity) if conservation was planned using the target biodiversity directly. The optimal curve plots the percentage of phylogenetic

or functional diversity represented as a function of area when grid cells are selected within spatial prioritizations targeting phylogenetic or functional features directly. Thus, the optimal curve represents maximum surrogacy—planning using a surrogate can never be more efficient than is possible using the target itself<sup>5</sup>. Second, the 'surrogacy curve' represents the accumulation of the target biodiversity (that is, phylogenetic or functional biodiversity) if conservation was planned using species diversity as a surrogate. The surrogacy curve displays the percentage of the target biodiversity represented when grid cells are selected within spatial prioritizations targeting species diversity. Third, the 'random curve' is generated by selecting a thousand sequences of grid cells at random, and assessing the representation of the target biodiversity (that is, phylogenetic or functional biodiversity) in each. These thousand runs allowed us to generate 95% CIs around a median 'random curve'. In addition, because we ran ten iterations of each spatial prioritization algorithm, optimal and surrogate curves were also summarized using the median and 95% CIs across the 10 iterations.

Importantly, because the three conservation strategies we used prioritized different aspects of species, phylogenetic or functional diversity (see Table 1), we assessed surrogacy for each strategy using different definitions of target biodiversity. For this purpose, we used the same metrics as Pollock et al.<sup>5</sup> (our equations (1)–(3) corresponding to the four equations in their Methods<sup>5</sup>). For 'Prioritize representation of all features', we defined target biodiversity simply as the percentage of phylogenetic or trait branches in the study area ( $N$ ) represented within the prioritized area ( $n$ ), with all branches weighted equally:

$$\frac{n}{N} \times 100 \quad (1)$$

For 'Prioritize representation of most range-restricted features', we estimated the total sum of the phylogenetic or trait branch lengths connecting species (that is Faith's phylogenetic diversity<sup>58</sup>) occurring within the priority areas over the total sum of the branch lengths of all species in the study area (that is, Faith's phylogenetic diversity<sup>58</sup> across all tetrapods in the study area) using equation (2):

$$\frac{\sum_{i=1}^P L_i}{\sum_{i=1}^P L_i} \times 100 \quad (2)$$

where  $p$  represents the phylogenetic or trait branches of all species included in the prioritized area,  $P$  is the full set of branches in the study area and  $L_i$  is the length of branch  $i$ .

For 'Prioritize areas with highest cumulative range-restriction across features', we assessed the prioritization of phylogenetic or trait branches using the percentage weighted endemism, weighted by the branch lengths:

$$\frac{1}{\sum_{i=1}^P L_i} \times \sum_{i=1}^P \left[ L_i \times \frac{\theta_i}{\Theta_i} \right] \times 100 \quad (3)$$

where  $P$  is the total number of phylogenetic or trait branches in the study area,  $L_i$  is the length of branch  $i$ ,  $\theta_i$  is the number of grid cells where branch  $i$  occurs within the prioritized area and  $\Theta_i$  is the total number of grid cells where branch  $i$  occurs across the study area.

Once the target, surrogate and random curves were calculated based on the appropriate target biodiversity definition, we derived the quantitative measure of surrogacy as  $SAI = (s - r) / (o - r)$ , where  $s$  is the area under the surrogate curve,  $r$  is the area under the random curve and  $o$  is the area under the optimal curve<sup>15,23,60</sup>. The SAI value is 1 when the optimal and surrogate curves are the same (perfect surrogacy). It is between 1 and 0 when the surrogate curve lies above the random curve (positive surrogacy), 0 when the surrogate and random curves coincide (no surrogacy), and <0 when the surrogate curve lies below the random curve (negative surrogacy). We calculated the SAI using the approach developed by Ferrier<sup>23</sup> and R code modified from Sabatini et al.<sup>61</sup>. Based on all spatial prioritization iterations we ran (10 for target and surrogate curves; 1,000 for random curves), we calculated SAI values for each potential combination of optimal, surrogate and random curves and report the median and 95% CIs over all values.

**Future surrogacy projection.** We used the Red List to project extinctions and associated loss of phylogenetic and functional biodiversity by assuming that all species categorized as vulnerable, endangered and critically endangered will go extinct. Therefore, our 'projected' surrogacy values are based on re-running all spatial prioritization and surrogacy analyses using all species within our study set (hereafter, labelled as 'current') minus those listed as vulnerable, endangered or critically endangered. Considerable uncertainty in the projections of surrogacy can result from the fact that we do not know the threat prevalence of data-deficient species<sup>63</sup>. To derive the absolute lower and upper uncertainty bounds to this uncertainty, we considered two scenarios for our projections: all data-deficient species are threatened or they are all non-threatened. Although more complicated ways exist to address this issue<sup>63</sup>, we did not deem these to be necessary for our purposes, because the absolute upper and lower bounds we considered generated very similar results.

**Surrogacy of regions of conservation importance.** We also assessed the surrogacy value of regions of conservation importance: the conservation value of the species included within each region for each dimension of biodiversity. Following recent studies<sup>14,15</sup>, we calculated this value using the SAI formula but, instead of comparing areas under curves, we extracted single values for: (1) the target biodiversity represented within each region (*s*); (2) the target biodiversity represented within a similar land area selected based on optimal accumulation of the target (*o*); and (3) the target biodiversity represented within a similar land area selected at random (*r*). Using this same approach, we also calculated SAI values for both phylogenetic and functional targets across all taxa for each 20% increment in the minimum percentage land cover required for each cell to be protected (from 10 to 90%); these values are summarized in Supplementary Table 6.

**Phylogenetic and functional distinctiveness.** Finally, to gain a better understanding of the phylogenetic and functional diversity that is not represented within species-based conservation plans, we quantified the total phylogenetic and functional distinctiveness of species not represented within species-based priority areas. First, we calculated the phylogenetic and functional distinctiveness of all species included in our study area using the measure of evolutionarily distinctiveness by fair proportions reported by Isaac et al.<sup>30</sup> applied to the tetrapod phylogenetic and functional trees, respectively. Second, we summed the phylogenetic/functional distinctiveness scores of species not represented within species-based priority areas of increasing size. We present these results in Fig. 3: this figure displays the decay in the total phylogenetic and functional distinctiveness of species missing from species-based conservation priority areas, expressed as a percentage of the summed distinctiveness of all species in the Americas-wide species pool. Moreover, to convey the outcome of a 'worst-case' scenario, Fig. 3 displays the maximum total phylogenetic/functional distinctiveness value calculated for any of the ten iterations we ran for each conservation plan.

**Reporting Summary.** Further information on research design is available in the Nature Research Reporting Summary linked to this article.

**Code availability.** All analysis R code is available in a dedicated GitHub repository at <https://github.com/giorap/surrogacy-among-biodiversity-dimensions>.

## Data availability

Distribution and extinction risk data for amphibians, birds, mammals and most reptiles are available through the IUCN Red List (<https://www.iucnredlist.org/resources/spatial-data-download>; for amphibians, reptiles and mammals) and BirdLife International (<http://datazone.birdlife.org/species/requestdis>; for birds). Phylogenetic data are available through the TimeTree of Life project (<http://www.timetree.org/>). Trait data were obtained from a number of existing data sources listed in the Methods. Distribution and extinction risk data for some of the squamate species of South America and the Caribbean are currently being processed by IUCN and will be provided shortly in the same format as that used for the other taxa (<http://www.iucnredlist.org> and <https://www.iucnredlist.org/resources/spatial-data-download>). All analysis R code, processed input data and summary output files are available in a dedicated GitHub repository at <https://github.com/giorap/surrogacy-among-biodiversity-dimensions>.

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## Author contributions

T.M.B., G.R. and C.H.G. designed the study with input from all other authors. G.R. and J.M. integrated and processed the datasets. G.R. conducted the analyses with input from T.M.B., C.H.G. and J.M. G.R. and T.M.B. wrote the initial manuscript draft. All authors contributed to editing subsequent manuscript versions.

## Competing interests

The authors declare no competing interests.

## Additional information

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Data collection

The vast majority of data used are openly available in online repositories. All data were obtained and processed in R and all R code for processing data will be made available upon acceptance of this work.

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All analyses were conducted in R and Zonation. Zonation runs were set up and started from within R using the R package zonator. All R code used for data analysis has been made available in the GitHub repository at <https://github.com/giorap/surrogacy-among-biodiversity-dimensions>.

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The vast majority of data used in our analyses have already been deposited in online repositories. Distribution and extinction risk data for amphibians, birds, mammals and most reptiles are available through IUCN (<http://www.iucnredlist.org/technical-documents/spatial-data>) and Birdlife (<http://datazone.birdlife.org/species/requestdis>). Phylogenetic data are available through the Timetree of Life project (<http://www.timetree.org/>). Trait data were obtained from a number of existing data sources listed in the Methods section of this submission. Distribution and extinction risk data for a few hundred squamate species of South America and the Caribbean are currently being processed by IUCN and will be provided shortly in a format akin to that used for other taxa (<http://www.iucnredlist.org>; <http://www.iucnredlist.org/technical-documents/spatial-data>). All processed input data files used to carry out the analyses in this paper have been provided in the GitHub repository at <https://github.com/giorap/surrogacy-among-biodiversity-dimensions>.

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## Life sciences

### Study design

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Sample size	Sample size was selected to represent all tetrapod species/phylogenetic/functional units across the Americas as exhaustively as is currently possible. We obtained data of all types for the majority of tetrapod species (77%) and families (88%) in the Americas.
Data exclusions	Exclusion criteria were not pre-established. 23% of tetrapod species in the Americas were not included in our analyses due to missing distribution, phylogenetic, functional and/or extinction risk data. We provide a full list of the species excluded in the GitHub repository <a href="https://github.com/giorap/good-surrogacy-among-biodiversity-dimensions">https://github.com/giorap/good-surrogacy-among-biodiversity-dimensions</a> , and a full list of the tetrapod families excluded in the new Supplementary Table 3.
Replication	We did not conduct experiments. However, our analyses are fully reproducible using the R code provided in the GitHub repository <a href="https://github.com/giorap/surrogacy-among-biodiversity-dimensions">https://github.com/giorap/surrogacy-among-biodiversity-dimensions</a>
Randomization	Not applicable
Blinding	Not applicable

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