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Limitations and trade-offs in the use of species distribution maps for protected area planning

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Summary

1. Range maps represent the geographic distribution of species, and they are commonly used to determine species coverage within protected areas and to find additional places needing protection. However, range maps are characterized by commission errors, where species are thought to be present in locations where they are not. When available, habitat suitability models can reduce commission errors in range maps, but these models are not always available. Adopting a coarse spatial resolution is often seen as an alternative approach for reducing the effect of commission errors, but this comes with poorly explored conservation trade-offs.

2. Here, we characterize these trade-offs by identifying scenarios of protected area expansion for the world's threatened terrestrial mammals under different resolutions (10–200 km) and distribution data deriving from range maps and habitat suitability models.

3. We found that planning new protected areas using range maps results in an overestimation of the species protection level when compared with habitat suitability models (which are more closely related to species presence). This overestimation increases when more area is selected for protection and is higher when higher spatial resolutions are employed.

4. Adopting coarse resolutions reduced the overestimation of species protection and also halved the spatial incongruence between protected areas prioritized from range maps or habitat suitability models. However, this came at a very high cost, with an area of up to four times greater (12 M km^2 vs. 3 M km^2) needed to adequately protect all species.

5. *Synthesis and applications*. Our findings demonstrate that adopting coarse resolutions in protected area planning results in unsustainable increases in costs, with limited benefits in terms of reducing the effect of commission errors in species range maps. We recommend that, if some level of uncertainty is acceptable to practitioners, using range maps at resolutions of 20–30 km is the best compromise for reducing the effect of commission errors while maintaining cost-efficiency in conservation analyses.

Key-words: commission errors, conservation planning, geographic range, habitat suitability model, IUCN range maps, protected area planning, spatial conservation prioritization, spatial resolution, species distribution, threatened species

Introduction

Conservation efforts at all scales are influenced by the knowledge of where species are distributed (Margules & Pressey 2000; Whittaker *et al.* 2005). Maps of the distribution of species are commonly used to determine their coverage within protected areas, and to find where new protected areas need to be placed (Venter *et al.* 2014; Watson *et al.* 2014; Butchart *et al.* 2015). These maps are also used to determine local-scale priorities for conservation actions (Wilson *et al.* 2007; Carwardine *et al.* 2008b). Similarly, the investigation of macroecological patterns is

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necessarily based on our knowledge of past and present species distributions (Orme *et al.* 2006; Di Marco & Santini 2015; Faurby & Svenning 2015).

Long-standing debate has focused on the most appropriate methodologies to follow for creating and using distribution maps in conservation and ecological analyses (Rondinini *et al.* 2006; Gaston & Fuller 2009; Guisan *et al.* 2013; Joppa *et al.* 2015). In addition, recent international commitments to expand the global protected area (PA) network (Watson *et al.* 2014) are stimulating ever increasing research on the use of species distribution maps to inform PA expansion (McCarthy *et al.* 2012; Montesino Pouzols *et al.* 2014; Venter *et al.* 2014; Butchart *et al.* 2015). Underpinning much of this work are geographic ranges, or simply 'ranges', mapped by the Red List of the International Union for Conservation of Nature (IUCN). These are the most comprehensive (taxonomically and geographically) data on the global distribution of tens of thousands of species (IUCN 2015). These maps have been repeatedly used in global and regional conservation analyses, often to identify gaps in PA coverage and priorities for PA expansion (Rodrigues *et al.* 2004; Venter *et al.* 2014).

Despite the increasing completeness and availability of species range data sets, our knowledge of the geographic distributions of species remains inadequate (Whittaker *et al.* 2005; Pimm *et al.* 2014). A key issue is that range maps are coarse representations of species distributions, and they are particularly prone to commission errors, where species are thought to be present in locations where they are actually absent (Rodrigues *et al.* 2004; Rondinini *et al.* 2006; Jetz, Sekercioglu & Watson 2008). This issue can have significant impacts on how conservation priorities are set. Commission errors can result in an overestimation of PA coverage for some species and can lead to the identification of priority areas that do not actually contain the species that triggered the priority listing. In addition, overestimating species distributions can result in an overoptimistic assessment of their extinction risk if the actual ranges are substantially smaller than expected. Range maps are also prone to omission errors, that is overlooking areas which are actually occupied by the species. However, these errors are not analysed here, since they are mostly relevant for groups with localized distributions, such as amphibians, and their influence in conservation assessments has already been discussed elsewhere (Ficetola *et al.* 2014).

Two main approaches have been adopted to deal with commission errors when using species range maps: (i) performing analyses at a coarse resolution and (ii) using refined habitat suitability models. In the first case, coarse grid resolutions are used, for example 1 or 2 degrees (Hurlbert & Jetz 2007), to reduce the probability of including unoccupied grid cells as part of a species' distribution. This is not in itself a solution to the problem, rather it is a way to minimize its effects. A wide spectrum of spatial resolutions are still commonly employed for analysing species range maps, with the most common values ranging from 10 km (Wilson *et al.* 2011) to 200 km (Hurlbert & Jetz 2007) grid cells. This heterogeneity in resolution has important theoretical and practical conservation implications. In the second case, commission errors are reduced by removing unsuitable habitat from species range maps, using expert-based or statistically derived relationships between species presence and environmental characteristics (Rondinini, Stuart & Boitani 2005; Jetz, Wilcove & Dobson 2007). This way, the likelihood of including unoccupied areas in a conservation plan can be much reduced, thus minimizing the likelihood of commission errors.

Habitat suitability models, or extensive survey data (Di Marco *et al.* 2016), are not always available, and therefore coarse spatial resolutions are often employed when using range maps suffering from commission errors (Hurlbert & Jetz 2007). The effect of changing resolution when using range maps for analysing macroecological patterns (such as species richness) has been investigated (Rahbek 2005; Pineda & Lobo 2012). Similarly, the effect of overestimating species ranges due to commission errors has been assessed at different scales (Jetz, Sekercioglu & Watson 2008). However, the trade-off associated with the use of different spatial resolutions and how these are influenced by different species distribution proxies (e.g. habitat models vs. range maps) is yet to be investigated in the context of conservation planning. Assessing this trade-off will allow conservation decision-makers to better navigate the decision between increasing the efficiency of a conservation plan, by performing analyses at a fine resolution, vs. reducing uncertainty in the use of range maps with commission errors, by performing analyses at a coarse resolution. After decades of development of species distribution maps, guidelines of how to use these maps for conservation planning are still missing.

We measured the effect of different spatial resolutions on the identification of priority areas for PA expansion, using different distribution proxies – IUCN range maps and habitat suitability models – to measure species coverage within PAs. We employed analytical resolutions ranging from 10 km to 200 km (Fig. 1), which are typically used in global conservation and ecological analyses (Ceballos *et al.* 2005; Hurlbert & Jetz 2007; Carwardine *et al.* 2008a; Wilson *et al.* 2011; Venter *et al.* 2014). We focused our analyses on threatened terrestrial mammals, since both distribution data types (ranges and habitat models) are comprehensively available for this group and they represent, together with birds, the taxonomic group attracting the most attention in conservation science (Clark & May 2002; Lawler *et al.* 2006), providing a good study case for other groups. We identified priority areas for PA expansion using a conservation planning approach, where our aim was to find the minimum set of additional area to be protected in order to achieve an adequate level of coverage for all species.

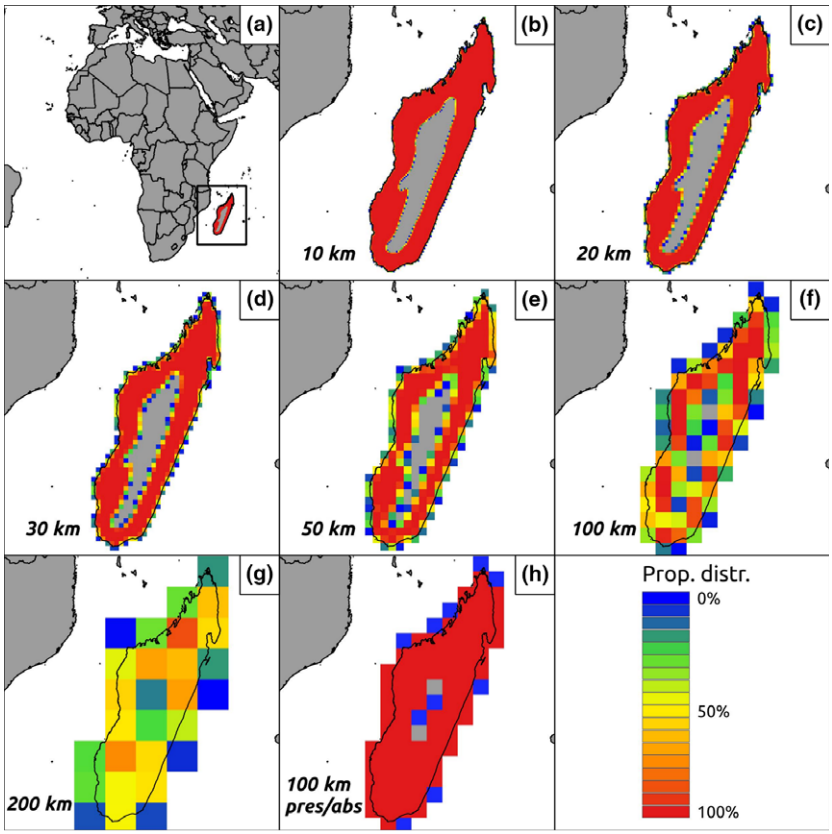

Fig. 1. Spatial distribution of the fossa (*Cryptoprocta ferox*), a threatened Madagascan mammal. Panel (a) shows the global location of the species range. Panels (b–g) show the proportion of species geographic range within grid cells at various resolutions (from 10 km to 200 km). Panel (h) shows a binary reclassification (presence/absence) of the species range at a 100 km resolution; in this case a cell was considered to be entirely occupied if ≥5% of its area overlapped with the species range, and entirely unoccupied otherwise. The colour scale is the same for all panels.

Materials and methods

DISTRIBUTION DATA

We analysed distribution data for 1115 (99·5%) species of threatened terrestrial mammals with available distribution information. Following previous studies (Venter *et al.* 2014), we focused our analyses on threatened species, because these are the species of highest conservation concern and typically targeted by international conventions (Secretariat of the CBD 2010).

We obtained geographic range maps from the IUCN Red List (IUCN 2015) and habitat suitability models from the Global Mammal Assessment program (https://globalmammal.org/habitat-suitability-models-for-terrestrial-mammals/). IUCN range maps represent the global distribution of species and include all areas where a species is found to occur permanently or periodically. Following previous works (Venter *et al.* 2014; Butchart *et al.* 2015), we removed areas where species exist outside their native ranges, and areas where species were considered to be extinct (i.e. areas that were part of the historical range but not part of the current range).

Range maps can include areas which are unable to sustain viable populations and are only used occasionally by the species (e.g. during dispersal movements). In contrast, expert-based habitat suitability models are deductive classifications of species habitat requirements, based on information retrieved from the literature, and allow the identification of suitable and unsuitable areas within the species ranges. The habitat suitability models used in our study were described in Rondinini *et al.* (2011), who employed a systematic classification of the species' habitat preferences reported in the IUCN Red List data base (IUCN 2015). The models were based on the following: species' preferences for land cover type and their tolerance to human settlements, mapped using Globcover (Bontemps *et al.* 2011); species' altitudinal limits, mapped from the Shuttle Radar Topography Mission elevation (USGS 2006); species' relationship with water bodies, mapped from Globcover and Vmap0 (National Imagery and Mapping Agency 1997). For 102 species in our sample (<9%), the entire range was considered suitable because they had a geographic range smaller than 100 km^2 (n = 83), which also corresponds to the smallest planning units size adopted in our spatial prioritization analysis (see below), or because the information on habitat preferences was missing (n = 19) (Rondinini *et al.* 2011).

We used the July 2015 version of the World Database on Protected Areas to measure the current level of species coverage within PAs (IUCN & UNEP-WCMC 2015). We considered all designated terrestrial PAs associated with an IUCN category of management (from I to VI). These included areas with a defined spatial shape (n = 125 430) and areas represented as buffered centroids (n = 11 997). All spatial maps (ranges, habitat suitability models and protected areas) were initially rasterized at a 300 m resolution, that is the native resolution of habitat suitability models. The maps were subsequently resampled at coarser analytical resolutions, using cell sizes typically employed in global-scale analyses: 10 km, 20 km, 30 km, 50 km, 100 km and 200 km. To resample the data at a coarser resolution, we measured the proportional species occupancy of each grid cell by overlapping high-resolution maps of species distribution and obtained continuous values ranging from 0 km^2 to the maximum of the cell size; a graphical representation of the resampling process is provided in Fig. 1. We also tested the effect of using a binary, rather than continuous, resampling technique, where each cell was considered

to be either occupied or not (Ceballos *et al.* 2005). In this case, we set a minimum threshold of 5% of the cell overlapping with a species' distribution map in order for it to be considered occupied, to exclude marginal overlaps from the analyses (Fig. 1h).

All spatial analyses were performed in a Mollweide equal-area projection, with the software GRASSGIS (GRASS Development Team 2014).

SPATIAL PRIORITIZATION ANALYSIS

We defined global grids at various resolutions (from 10 km to 200 km, described above) and resampled the distribution of species and PAs in each grid cell. For each grid cell, we measured the extent of species' geographic range and the extent of species' suitable habitat [including both medium and high suitability; (Rondinini *et al.* 2011)], within and outside of PAs. In this way, we were able to measure the total extent of protected and unprotected species distribution. We used the total distribution of species to calculate representation targets, following Rodrigues *et al.* (2004) and subsequent applications (Venter *et al.* 2014; Butchart *et al.* 2015), according to the following formulation:

$$\text{Target} = \text{MAX}\,(0{\cdot}1, \text{MIN}\,(1, -0{\cdot}375 \times \log 10(\text{range size}) + 2{\cdot}126))$$

Widespread species with a global geographic range larger than 250 000 km^2 were assigned a fixed target of 10%. Small-ranged species with a global geographic range smaller than 1000 km^2 were assigned a fixed target of 100%. Intermediate-ranged species were assigned a target value which was loglinearly interpolated between the two thresholds. The current PA coverage was used to calculate the shortfall between current level of protection and the desired level of protection (represented by the targets).

We performed global-scale spatial prioritization analyses to identify the places where the shortfall in current levels of species protection could be covered with a minimal additional area. We used Marxan (Ball, Possingham & Watts 2009), a spatial prioritization software, to identify spatial priorities for PA expansion. We treated grid cells as planning units, and let the new PAs be selected only among the unprotected portion of each grid cell. For each scenario and for each resolution (described below), we performed one Marxan run with one billion iterations and no boundary length modifier (Venter *et al.* 2014). We then defined a coverage curve by incrementally expanding the global PA network up to x km^2, where x is the total area required to achieve adequate PA coverage for all species (and x is different for different resolutions). For each increment, we measured the aggregate proportion of representation targets met, which we referred to as 'species coverage'. We also measured the level of spatial overlap between the priority areas identified under the three scenarios, at various resolutions (fine to coarse).

SCENARIOS SETTING

We defined three analytical scenarios, based on the use of habitat suitability models and geographic range maps to represent species distributions (Table 1). In the first scenario, 'perceived coverage', we used range maps to identify priority sites for PA expansion and to measure the achievement of species targets. We considered this coverage as 'perceived', as opposed to 'realized' (see below), because the presence of commission errors in range maps may result in an overestimation of the actual level of species coverage achieved. This is the scenario typically employed in global-scale spatial prioritization analyses (Rodrigues *et al.* 2004; Montesino Pouzols *et al.* 2014; Venter *et al.* 2014; Butchart *et al.* 2015).

In the second scenario, 'realized coverage', we used range maps to identify priority sites for PA expansion and habitat suitability models to measure the achievement of species targets. We considered this coverage as 'realized', because only the areas where the species is expected to occur are considered when measuring the achievement of targets. This corresponds to an evaluation of the actual coverage achieved (in terms of represented suitable habitat) when employing a coarse distribution proxy such as geographic range.

In the third scenario, 'suitable coverage', we used habitat suitability models to identify priority sites for PA expansion and to measure the achievement of targets. In this case, the priority sites for PA expansion are directly targeted to the representation of suitable habitat. This scenario is equivalent to targeting the areas where a species is most likely to occur, and measuring PA coverage only for these areas.

For each of the three scenarios, and for each separate resolution settings, we defined curves of the relationship between area covered and cumulative levels of species targets achieved (which we refer to as 'species coverage'). We also compared these scenarios with a 'random coverage' scenario, representing a null model of protected area expansion where no knowledge of species distribution is assumed. In this case, planning units were selected at random to achieve the same cumulative levels of protected area expansion as for the realized scenario. To represent the coverage achieved under this scenario, we defined 100 random planning unit samples for each cumulative level of protected area expansion and extracted the median coverage across all the samples.

SENSITIVITY TESTING

We verified the sensitivity of our results to alternative settings of the spatial resampling procedure and spatial prioritization analysis. In our analyses, we associated fine-grain information with each grid cell, in the form of proportional distribution data (i.e. proportion of species range within each grid cell). An alternative, and less time-consuming, approach would be to reclassify all data as binary presence/absence values, especially when coarse resolutions are adopted. To test the effects of this alternative approach, we adopted a binary resampling technique at a commonly used coarse resolution of 100 km (Ceballos *et al.* 2005). We also verified the sensitivity of our trade-off curves to the use of a different formulation of the species representation target, by applying fixed targets of 20% to all species (Di Marco *et al.* 2016), at a

Table 1. Scenarios of species coverage, obtained by the use of geographic ranges or suitable habitat models for spatial prioritization and for measuring species coverage (i.e. achievement of species' targets)

	Measuring coverage: range	Measuring coverage: suitable habitat
Spatial planning: range	Perceived coverage	Realized coverage
Spatial planning: suitable habitat	N/A	Suitable coverage

commonly used intermediate resolution of 30 km^2 (Venter *et al.* 2014). Finally, we verified whether our trade-off curves showed a consistent pattern when using agricultural opportunity cost (Naidoo & Iwamura 2007), rather than total land area, as a cost layer for the spatial prioritization.

Results

We found that 165 out of 1115 threatened terrestrial mammals have a geographic range already adequately covered with PAs, meaning that their proportional representation targets are already achieved, while 247 species have an extent of suitable habitat already adequately covered with PAs. When plotting the relationship between protected area expansion and increased species coverage, we found similar nonlinear shapes under all the scenarios and for each analytical resolution (Fig. 2). These curves showed that a high level of species coverage is achievable with a small efficient expansion of the protected area network, in contrast to the small linear increase in coverage that would be expected under a null model of PA expansion (Fig. S1, Supporting Information). We found that the realized level of coverage from new PAs, measured using habitat suitability models, was lower than the perceived level of coverage (Fig. 2). This difference was evident when >30% of the total PA expansion was reached, and increased with increasing PA expansion, until the complete perceived coverage was achieved. For example, at a resolution of 10 km the difference between perceived and realized coverage corresponded to 14 species with a PA expansion of 1·3 million km^2 and 28 species with an expansion of 3·1 million km^2.

The gap between perceived and realized coverage introduces a level of uncertainty regarding which and how many species will be adequately covered when planning new PAs using range maps. The suitable level of coverage, obtained using habitat suitability models, was always higher than the perceived and realized levels for a similar cost. This highlights the fact that suitable habitat is not randomly distributed within the species ranges, and selecting a few highly suitable planning units would allow a rapid achievement of the species targets. This also indicates that planning new PAs using species range maps results in a coverage which is lower than expected, and lower than possible if using refined information on where species are most likely located.

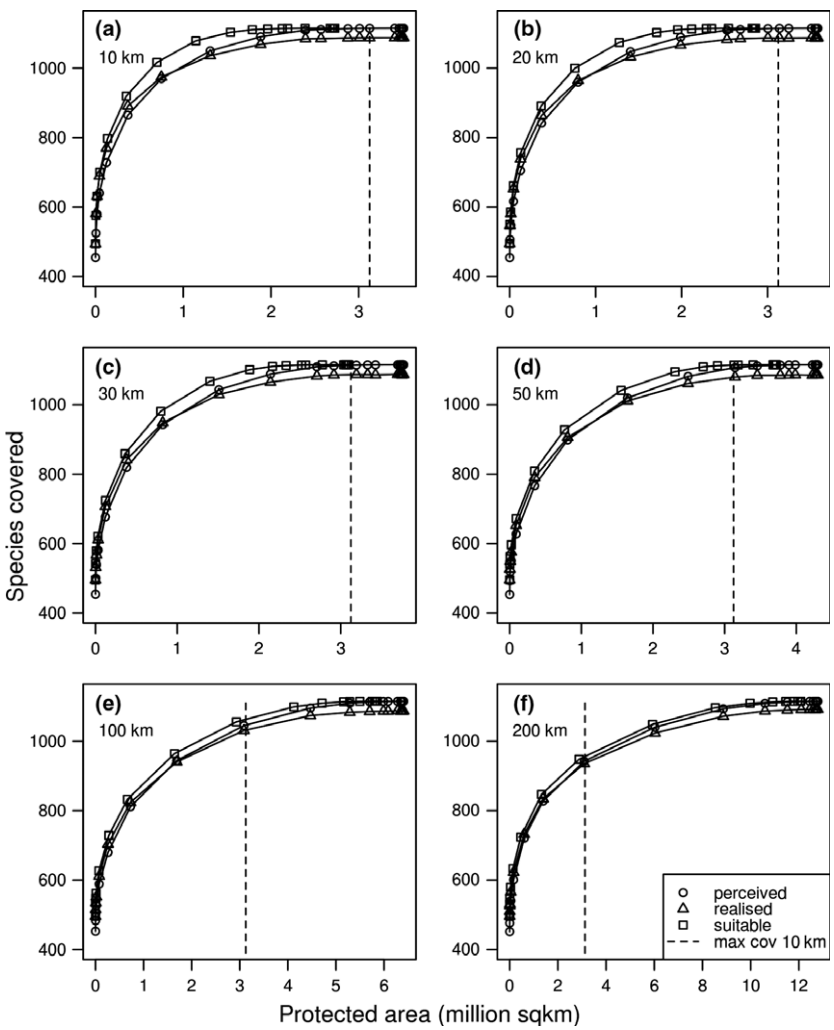

Fig. 2. Trade-off between total area prioritized for protection and aggregate level of species coverage (i.e. sum of species targets achieved). The trade-off curves represent the three scenarios (perceived, realized and suitable) described in Table 1. Data in plots (a–f) refer to different analytical resolutions, as specified in the plot. Note that the *x-axes* in different panels have different scales, and the dashed vertical line represents the minimum area required to achieve maximal coverage at a 10-km resolution (reported in all panels for reference).

There were some benefits though to employing coarser analytical resolutions, which tended to lead to a slightly reduced level of uncertainty in the use of range distribution data. This reduced uncertainty was represented by a higher level of correspondence between the perceived and the realized levels of coverage (Fig. 2). In fact, expanding the global PA network by 3·1 million km^2 at a 10-km analytical resolution resulted in a perceived level of coverage of 1115 species (i.e. all species targets were met), and a realized level of coverage of 1087 species (difference = 28 species). When applying the same extent of PA expansion (i.e. 3·1 M km^2) under a 200-km resolution, the difference in coverage between these two scenarios was reduced to 7 species (perceived = 942 species, realized = 935 species).

Importantly, the use of coarser analytical resolutions resulted in a substantial increase in the area required to meet species targets. When analyses were performed at a 10-km resolution under the perceived coverage scenario (i.e. based on range maps), we found that 3·1 million km^2 of additional PAs were required to achieve an adequate coverage for all species. In contrast, when a 200-km resolution was employed, we found that a fourfold increase in the additional reserve area (12·1 million km^2) was required to achieve an adequate coverage for all species. We found a nonlinear relationship between the use of a coarser analytical resolution and the total area required to achieve the desired level of species coverage, both under the perceived coverage scenario and the suitable coverage scenario (Fig. 3). The difference between these two scenarios was larger at a resolution of 10 km and smaller at coarser resolutions, while the increase in the total area required was higher for resolutions coarser than 30 km.

We mapped the spatial priorities for PA expansion required to achieve complete species coverage under the perceived (i.e. range based) and suitable (i.e. habitat based) scenarios (Fig. 4, see also Figs S2–S4). Spatial priorities determined a partial overlap between the scenarios, identifying three cases: areas selected only under the perceived scenario, areas selected only under the suitable scenario and areas selected under both scenarios (i.e. shared solution). A relationship was observed between coarser analytical resolution and increased amount of shared solution. In particular, analyses performed at a resolution of 200 km resulted in proportionally twice as much protected area being shared between the perceived and suitable scenario with respect to analyses performed at a 10-km resolution. This means that analyses done at a coarser resolution were less likely to produce spatial mismatch when using different types of distribution data (range maps or habitat models).

When reclassifying distribution data as binary presence/absence values, we observed a large difference (an overestimation) in the measure of perceived species coverage. In fact, a much higher level of perceived species coverage was found when using presence/absence data rather than proportional distribution data, for the same increment of PAs (Fig. S5). This is due to the consideration of cells as being entirely occupied by a species, when at least a significant portion was occupied. This means that, under a naive resampling technique, many species might be perceived to be adequately covered with PAs when they are actually not. When employing a fixed target formulation (20% for all species) for identifying priorities for PA expansion, we did not find a significant change in the shape of the area–coverage relationships or in the respective position of the scenarios in the plot (Fig. 5). The only noticeable difference with respect to the use of proportional targets scaled with range size was that in this case the scenarios achieved near-complete levels of coverage much more rapidly. For example, coverage of 1039 species was achieved with a PA expansion of 715 thousand km^2 under the fixed target formulation, while only 943 species were covered with a PA expansion of 822 thousand km^2 under a scaled target formulation. However, the achievement of complete coverage (i.e. all 1115 targets met) required a larger area under the fixed target formulation (5·8 million km^2) than under the scaled target formulation (3·3 million km^2). Finally, we did not find substantial differences in the trade-off curves when using agricultural opportunity cost (instead of spatial extent) as a surrogate of PA expansion cost (Fig. S6).

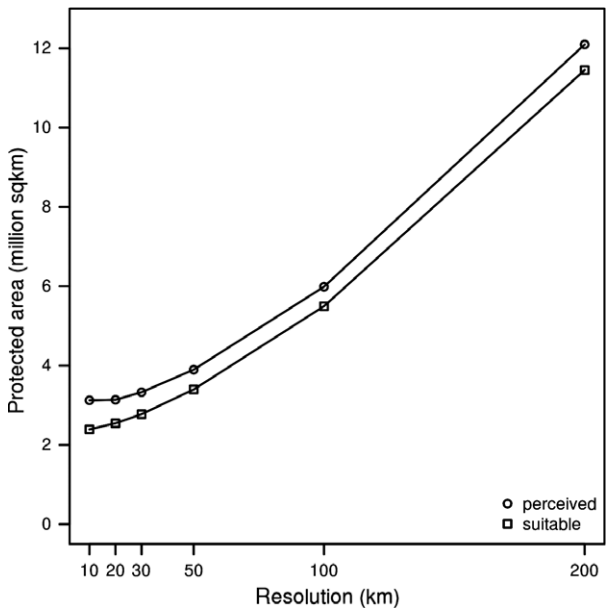

Fig. 3. Relationship between the analytical resolution employed and the total protected area required to achieve the desired level of species coverage. Both the perceived coverage scenario, based on species ranges, and the suitable coverage scenario, based on habitat suitability models, are represented.

Discussion

In this study, we systematically investigated the shortfalls and proposed approaches for use of species range maps

with commission errors. Our results illustrate a clear relationship between analytical resolution, data type, uncertainty in measuring PA coverage and cost-effectiveness of a spatial prioritization plan. We found that using species range maps at coarse vs. fine analytical resolutions has important conservation implications and trade-offs. At finer analytical resolutions, the spatial prioritization was very efficient in identifying the most strategic areas for PA expansion and required less total area to meet all species representation targets. However, we also discovered that this increased efficiency was associated with slightly higher uncertainty in the use of range maps, resulting in a perceived level of coverage higher than the realized level of coverage (as measured on suitable habitat). At coarser analytical resolutions, up to four times more area had to be selected to achieve complete species coverage, but the uncertainty associated with the use of species range maps was reduced. This has significant ramifications for planners using range maps for conservation applications: although a coarser resolution reduces the uncertainty deriving from commission errors, it also leads to a much larger area being selected to achieve the same level of protected area coverage for species. Moreover, this does not necessarily imply that a much larger suitable area is selected.

The identification of spatial priorities for PA expansion resulted in partially different areas being selected when using geographic range maps or habitat suitability models. Importantly, the mismatch in these spatial configurations was higher at finer resolutions and lower at coarser resolutions. This means that the spatial uncertainty associated with the use of geographic range maps is generally more evident at a local scale, while there is less uncertainty in the identification of larger regions at a broader scale. However, because conservation actions are typically implemented at a local scale (Boyd *et al.* 2008), the

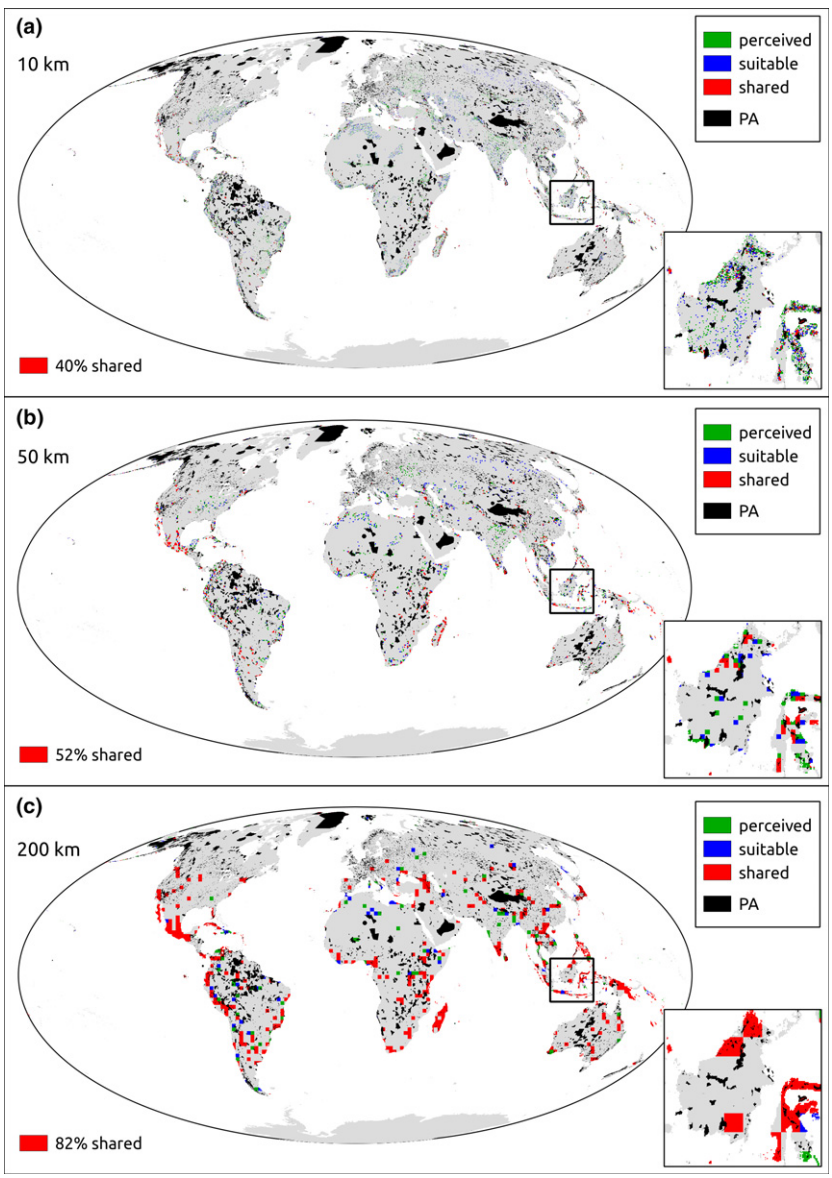

Fig. 4. Spatial solutions to achieve species representation targets under the perceived and suitable scenarios. Under both scenarios, the solution able to achieve complete species coverage with a minimum area was selected. Some of the grid cells are selected only under the perceived scenario or the suitable scenario and others are selected in both scenarios and thus part of a 'shared' solution. The numbers reported on the bottom left of each panel refer to the percentage area of the perceived scenario, which was also selected under the suitable scenario (i.e. the shared solution). Panels refer to results obtained under the following analytical resolutions: (a) 10 km; (b) 50 km; (c) 200 km. An inset map, with details of the South-East Asian region, is reported on the bottom right of each panel for visual reference. A larger version of the maps is reported in Figs S2–S4.

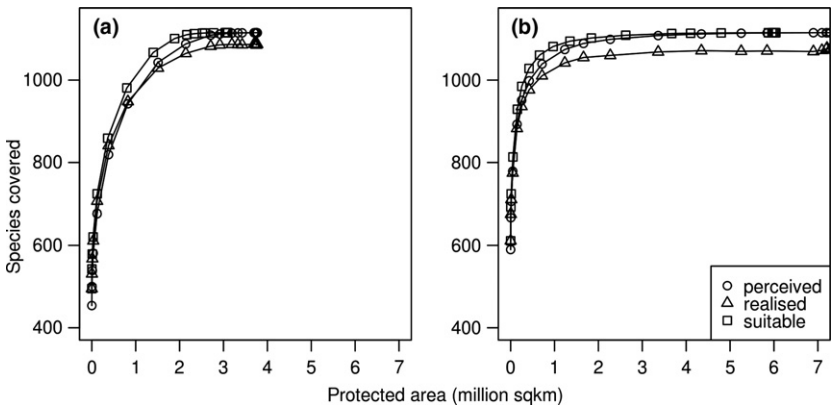

Fig. 5. Trade-off between total area prioritized for protection and aggregate level of species coverage (i.e. sum of species targets achieved) when employing different target formulations. The trade-off curves represent the three scenarios (perceived, realized and suitable) described in Table 1. Data in different plots refer to spatial priorities obtained under different target formulations: (a) proportional representation targets scaled to species range size and (b) fixed (20%) proportional representation targets applied to all species. Analyses were performed at a resolution of 30 km.

concordance of priority patterns at a very coarse resolution is likely to have little practical advantages.

Similar to previous studies (Venter *et al.* 2014), we found a nonlinear relationship between incremental PA coverage and incremental coverage of species distribution (i.e. a curve). In this relationship, high levels of species coverage are rapidly achieved when a relatively small amount of strategically located PAs is added to the network. However, to achieve complete coverage (i.e. all species adequately covered with PAs), a relatively large area is required. We found very similar curves when employing fixed representation targets or scaled representation targets, and when adopting land area or agricultural value as surrogate of PA costs. This indicates that our results were robust to the perturbations to the planning problem (i.e. different definitions of targets and costs). Under fixed, rather than scaled, targets, the species rapidly reached a near-complete coverage and then slowly progressed to complete coverage. This is related to the fact that the vast majority of species (80%) were associated with a scaled target larger than the adopted fixed target (20%). As a consequence, the spatial selection algorithm required less area to achieve the fixed target of these species. However, the remaining species had a scaled target lower than the fixed target (down to half of it). Achieving a 20% fixed representation target for these widespread species was spatially demanding, consequently almost twice as much area was necessary in the end to achieve complete coverage under the fixed target formulation.

Preventing the decline and extinction of threatened species is a priority goal for conservation interventions (Venter *et al.* 2014) and an explicit target of international biodiversity conventions (Secretariat of the CBD 2010). Terrestrial mammals represent one of the best studied animal groups and a perfect case for our analyses, since comprehensive distribution ranges (IUCN 2015) and habitat suitability models (Rondinini *et al.* 2011) are available for these species. This allowed us to identify trade-offs in the use of distribution maps at different analytical resolutions which can be applied to groups with less information available. The use of habitat suitability models allowed us to remove a substantial part [45% on average (Rondinini *et al.* 2011)] of the unsuitable habitat found within the geographic range of mammal species. This unsuitable habitat is likely associated with the perception of false presence (commission error). We acknowledge that habitat suitability maps are model outputs and thus are also prone to some level of commission error, in case the species are not present in suitable habitat (Brooks, da Fonseca & Rodrigues 2004). However, this issue is much less prominent in habitat models than in range maps, as demonstrated through independent validation (Rondinini *et al.* 2011; Maiorano *et al.* 2013). Ultimately, the usefulness of high-resolution models depends on the quality of data used to build them (Rondinini *et al.* 2006), and that collection of new data on distribution and habitat will improve the quality of these maps and their efficiency for conservation.

In our paper, we did not deal with omission errors (false absences), which may be caused by a species occupying areas outside its mapped geographic range. This is acceptable for mammal species, for which commission errors are the main issue. For groups characterized by a more limited knowledge of their distribution, such as amphibians, the level of omission error can be more substantial (Ficetola *et al.* 2014). In this case, an additional trade-off element will be present in the choice of an appropriate analytical resolution, and it may be necessary to extend species range maps by a certain buffer around known locations, to avoid overlooking areas of potential species presence (Ficetola *et al.* 2014). Previous analyses showed that the use of habitat suitability models can introduce omission errors within a species' range (Beresford *et al.* 2011), if species occupy habitats classified as unsuitable. While commission error can lead to a false sense of species coverage with protected areas, omission errors can reduce the options available for additional protection. However, it has been argued that the former have much higher associated risk than the latter for protected area planning (Rondinini *et al.* 2006), potentially driving conservation investments towards areas where species are not actually present. The use of species distribution models, rather than expert-based habitat suitability models, can allow controlling the balance between commission and omission errors, by selecting thresholds to define suitable vs. unsuitable habitat (Guisan *et al.* 2013). However,

these models are more data demanding and are typically available only for a subset of species, rather than entire species groups.

Errors in spatial data sets (e.g. distributions of species, habitats or protected areas) need careful consideration, as these can lead to misleading assessments of conservation progresses (Visconti *et al.* 2013). It has been suggested that species range maps should be analysed at a coarse resolution (e.g. 2°, ~ 200 km) when investigating macroecological patterns (Hurlbert & Jetz 2007), in order to avoid misleading results due to the overestimation of actual species occupancy. Our results demonstrates that a coarser analytical resolution would also lead to reduced uncertainty in conservation analyses, both in terms of reduced overestimation in species PA coverage and in terms of reduced mismatch between spatial priorities identified using range or habitat models. However, we also found that performing analyses at a coarse resolution is highly inefficient when the objective is to identify spatial priorities for PA expansion. Achieving the desired level of species coverage at a resolution of 200 km required a PA expansion of 12·1 million km^2, four times more than when using a 10-km resolution. This would lead to unnecessarily high expenditure in PA expansion and could present a serious barrier to conservation efforts, since that figure is six times larger than what world governments have currently committed to in terms of terrestrial PA coverage (Secretariat of the CBD 2010; Juffe-Bignoli *et al.* 2014).

For regional- and global- scale conservation analysis of well-studied groups, such as mammals, we suggest that employing a relatively high analytical resolution (such as 10 km) and using refined distribution models is the most appropriate choice (Kark *et al.* 2009; Wilson *et al.* 2011). For less well-studied groups, habitat suitability models might not be comprehensively available and in this case coarser resolutions, 20 or 30 km, in combination with range maps should be employed (Montesino Pouzols *et al.* 2014; Venter *et al.* 2014; Butchart *et al.* 2015); these resolutions represent a good compromise to reduce the effect of commission errors with only little increase in the total protected area selected. We recommend that conservation analyses are not performed at very coarse resolutions (e.g. 100 km or more), as these are likely to produce highly cost-inefficient spatial plans. Conservation is an applied discipline and scientists are increasingly seeking for cost-efficient PA plans (Carwardine *et al.* 2008a; Venter *et al.* 2014). Hence, keeping costs substantially low is more important than having a partial reduction in the uncertainty deriving from commission errors.

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Data accessibility

All the data used in this study derive from external sources:

The species distribution ranges were derived from the IUCN Red List of Threatened Species, available at http://www.iucnredlist.org/technical-documents/spatial-data.

The protected areas data were derived from the World Database on Protected Areas (WDPA), available at: www.protectedplanet.net.

The habitat suitability models were derived from the Global Mammal Assessment programme, available at: http://globalmammal.org/habitat-suitability-models-for-terrestrial-mammals.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Fig. S1. Trade-off between total area prioritized for protection and aggregate level of species coverage under the three scenarios (perceived, realized and suitable) described in Table 1 and a 'random coverage' scenario.

Fig. S2. Spatial solutions to achieve species representation targets under the perceived and suitable scenarios at a resolution of 10 km.

Fig. S3. Spatial solutions to achieve species representation targets under the perceived and suitable scenarios at a resolution of 50 km.

Fig. S4. Spatial solutions to achieve species representation targets under the perceived and suitable scenarios at a resolution of 200 km.

Fig. S5. Performance of two planning scenarios in which the species distribution data were degraded to logic binary values of presence and absence.

Fig. S6. Trade-off between 'costs' of protected area (PA) expansion and aggregate level of species coverage (i.e. sum of species targets achieved) when employing different cost formulations.