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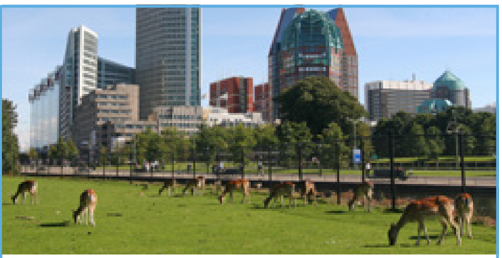

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Using Minimum Area Requirements (MAR) for assemblages of mammal and bird species in global biodiversity assessments

Abstract

Habitat loss, fragmentation and degradation are important factors in the decline of biodiversity worldwide. It is important to be able to evaluate the success of policies at different levels, including, increasingly, the global level. Whilst attention has been given to the development of predictive models that focus on individual species within biogeographic regions or smaller areas, however, to assess the impact of land-use change and policy measures on biodiversity at global level, there is an urgent need for generic tools (models, algorithms, databases). In this paper we test the potential of a generic tool, as part of the GLOBIO model, for assessing the impact of habitat loss and fragmentation. It combines existing data for the minimum viable populations of terrestrial bird and mammal species with knowledge of individual area requirements to derive estimates of their minimum area requirements (MAR). This approach focuses on comparing the minimum area requirements (MAR) to the natural habitat areas, assuming that below a certain threshold populations are no longer viable and the species assembly will eventually be reduced. The relationship between nature area and percentage of species meeting Minimum Area Requirements appears to be log-linear between 10 km^2 and 10 000 km^2 for conservation priority species and has the form Y=-15.45 + 28.61* LOG(AREA). Our results suggest that many existing parks and reserves might be too small for the long-term viability of species that they are meant to preserve. Applying this relationship to a global land cover dataset reveals that substantial proportions of mammal and bird species occur in areas that fail to cover sufficient space to support long term viable populations. This applies even at current state, especially for those areas of the globe where rapid urbanisation and agricultural expansion have taken place and are anticipated to proceed.

Introduction

The importance of conserving biodiversity in face of its decline is recognized by governments, organizations and international agreements. The Convention of Biological Diversity [1] had set a target to significantly reduce the rate of biodiversity loss by 2010, but this target was not met [2]. At the tenth meeting of the CBD Conference of the Parties held in Nagoya, Japan, in 2010 (in the Aichi Prefecture), a revized and updated Strategic Plan for Biodiversity was adopted, including the 'Aichi Biodiversity Targets', for the 2011-2020 period. This process has led to the formulation of five new goals and 20 specific targets within the updated strategy that aim at reducing biodiversity loss and promoting its sustainable use. Under Strategic Goal B ('Reduce the direct pressures on biodiversity and promote sustainable use'), Target 5 ('Habitat loss, fragmentation and degradation is significantly reduced') states that 'By 2020, the rate of loss of all natural habitats, including forests, is at least halved and where feasible brought close to zero, and degradation and fragmentation is significantly reduced' (http://www.cbd.int/decision/cop/?id=12268).

But how do we assess the potential of strategies (policies, measures) to meet these targets? Scientifically sound tools such as models, databases and algorithms are needed in order to be able to (i) assess the impact of environmental change resulting from on-going human population growth and economic development, and to (ii) evaluate the effectiveness of relevant environmental policy and measures in achieving their target [3]. National Biodiversity Strategies and Action Plans (NBSAPs) are the principal instruments for implementing the Convention of Biological Diversity at the national level (http://www.cbd.int/nbsap/); however, since policy decisions and measures in one place and time can affect biodiversity elsewhere (e.g. in other countries and continents), and have the potential to project their impacts into the future, global biodiversity assessment tools and a long-term perspective are needed to quantify and predict such effects. Biodiversity monitoring [4] and assessment tools are therefore required at different scale levels in order to shape nature policies and to prioritize actions from local to global [5]. The GLOBIO3 model was developed by the GLOBIO consortium, in response to the requirement for global level assessment (http://www.globio.info/home). The GLOBIO3 is a modelling framework for calculating the impact of environmental drivers on biodiversity for past, present and future scenarios. It is based on cause-effect relationships, derived from the literature and uses spatial information on environmental drivers as input. The model that we introduce, test and evaluate in this paper provides the scientific underpinning for one of the modules of the GLOBIO3 framework, dealing with the effect of habitat loss and fragmentation.

Large, relatively undisturbed areas of natural habitat play a major role in biodiversity conservation. On-going habitat loss has been identified as one of the main drivers of species extinction on local, regional and global scales [2,3,6]. Conversion of natural area into urban or agricultural land-use of low suitability to a large range of original species, can result in remaining habitats that are too small and/or too isolated to accommodate long-term viable populations.

Small and range-restricted populations are highly vulnerable to extinction [7-10]. Demographic stochasticity can cause chance extinction when numbers decline. Environmental stochasticity and catastrophic events can cause declines to low numbers and expose populations to further demographic extinction [11,12]. Moreover, inbreeding and loss of heterozygocity can decrease fitness in small and isolated populations and enhance vulnerability to environmental stress [13].

For long-term viability, populations need a certain minimum size. In 1981, Shaffer introduced the term ‘minimum viable population’ size (MVP), being ‘*the smallest isolated population having a 99% chance of remaining extant for 1000 years despite the foreseeable effects of demographic, environmental, and genetic stochasticity, and natural catastrophes*’ [14]. Since the 1980’s many studies have been published about the MVP concept, see for recent reviews Flather *et al*. [15] and Traill *et al*. [10]. A time horizon of 100 years and an extinction risk of 5% became the most frequently used criteria in the operational use of MVP [12,15].

However knowing how many individuals are needed for a minimum viable population is not sufficient for conservation planning. Shaffer [14,16] further defined the ‘minimum area requirement’ concept (MAR) as the minimum area suitable to accommodate a MVP. The MAR can be used as a threshold value for conservation, such as determining whether natural areas are large enough to accommodate viable populations of species. We argue that for biodiversity conservation, the mere presence of a species is not enough - although species can endure for long periods in areas that are too small for long-term survival, due to extinction debt [6] or just good luck. Instead, this study proposes that the MAR of conservation target species should be met to ensure long-term persistence. Recently, Pe’er *et al*. [17] noted that the MAR is provided and used far less often than the MVP, whereas MAR is potentially more useful for guiding conservation policy and management toward the goal of ensuring the long-term persistence of species.

Until now the MAR concept has mainly been applied in a single-species approach. Allen *et al*. [18] were the first to attempt compiling MAR values for an assemblage of species: a range of mammal species in Florida. Yet this was done by setting MVP to an arbitrary fixed value of 50 for all species and, thus, disregarding inter-specific differences in MVP. Systematic collation of MAR estimates, explicitly taking into account species traits, remains scarce. Only two studies known to us addressed these issues [17,19], both indicating a need to proceed further on the move from generalizations to decision-support.

This paper therefore takes a next step in moving from single-species estimations toward multiple species and biodiversity assessment. By converting MVP estimates of multiple species into area-based, and hence more policy-relevant, estimations, we allow spatial analyses and the production of maps that can be used for directing planning and policy. We take a minimalistic approach which involves various simplifying assumptions, but attempts to demonstrate the potential power of the actual conversion into maps for better visualization and communication of species needs. Thereby, we bring together three lines of research. First, we combine minimum viable population theory and data with recent findings on individual area requirements. We take the MVP database collected by Traill *et al*. [10] as a starting point, moving from MVP to MAR by adding individual area requirements based upon relations found in macro-ecological studies [20]. Second, we build upon the idea of moving from single species to species assemblies [18], not only by compiling a database of MAR values, but, additionally, by focusing on the systematic collation of species specific estimates using a standardized approach. Third, we bring a spatial approach which offers a potential replacement to the "species area relation" (SAR) approach. The SAR approach to link area to a biodiversity index [21-23], is not taking population viability into account, and therefore the long-term perspective is missing. Using a method for quantifying the relationship between patch size and the percentage of species of conservation interest meeting MAR, as a proxy for 'biodiversity' or ecosystem integrity [24] (0-100%), we incorporate long-term viability into a field which so far only asked 'how many do we obtain' but not 'how much is enough'. The idea behind our proposed metric is that a complete, intact ecosystem should be large enough to harbour an MVP of the most area demanding species (i.e., largest MAR). For areas below this threshold, our approach enables quantifying what fraction of species is expected to be maintained or lost, within a certain time horizon – as well as visualizing this information by converting it into maps. Such a conversion enables global assessments with a focus on long term viability.

A proxy for biodiversity, or ecosystem integrity, ranging from 0 to 100% and based on aggregated MAR values of conservation priority species can be derived from the relation between natural area size and the cumulative proportion of species with long-term viability perspectives. With the right selection of species, this proxy can be used as a biodiversity indicator by governments and NGOs in supporting biodiversity policies. The resulting relationship between area and this biodiversity proxy is part of the GLOBIO3 model (www.globio.info). The model combines the area relationship with other pressures [25-27]. The relationship can also be used in other frameworks, such as the ROBIN indicator framework (http://robinproject.info). The indicator yields a value of is 100% for a pristine state, while habitat loss and fragmentation reduce the value down to 0 when the environment is completely dominated by anthropogenic infrastructure. We show an example of applying this indicator in a global assessment.

In this paper we aim at deriving standardized Minimum Area Requirement estimates for a set of terrestrial birds and mammals. Next, we aim at demonstrating the use of these MAR estimates to produce a cumulative graph for multiple species, visualizing the information, and comparing the needs of species and communities with the remaining natural area in a given region. We also derive a general formula based upon these data. Finally, we aim at demonstrating the value of this general relationship between area and cumulative MAR and it's potential as a tool for nature conservation decision makers by applying this relationship at a global level for current land cover patterns and for a future projection, and discuss the potential merits and limitations of this approach for global biodiversity assessments. We achieved those aims and give suggestions for further improvements.

Material and Methods

The species specific Minimum Area Requirements (MAR) can be calculated by multiplying the area that one individual requires with the number of individuals required for a viable population (MVP) (Equation 1). There are two alternatives for estimating individual area requirements: using empirical data for home range size or for population density. This results in the following formulas:

$$MAR_{species\ i} = 0.5 * home\ range\ size_{species\ i} * MVP_{species\ i} \tag{1a}$$

$$MAR_{species\ i} = MVP_{species\ i} / density_{species\ i} \tag{1b}$$

Equation 1a is taken from Allen *et al* [18], where the division by two accounts for the presence of two sexes, assuming a 1:1 sex ratio and completely overlapping home ranges. There is however recent evidence that densities, in spite of variation in time and space, are more reliable than home range sizes when it comes to estimating the area requirements of populations, especially for large animals which may have considerable home range overlap [17,20,28,29]. Therefore we use the alternative Equation 1b for mammals, for which good density estimates are available, while using 1a for birds, for which this information is lacking. We first discuss the two components, MVP and individual area requirements, separately.

Towards a standardized MVP dataset

A MVP is the minimum population size to survive T years (or generations) with probability *p*. Estimates of MVP typically set the extinction probability at values from 5% to 1% and the time horizon at 50, through 100 to 1000 years, with no consensus on a set threshold for time horizon or extinction probability [10,15,17,30]. Studies also differ with respect to whether they include factors such as inbreeding and catastrophes in their analyses, and if so how. For a consistent dataset, standardization is therefore necessary. As a starting point we therefore use the MVP dataset collected by Traill *et al*. [10], who summarized 30 years of MVP-studies (141 sources and 212 species) in a meta-analysis, and proposed a standardisation formula derived by statistical analysis of the original MVP studies. The selected, highest ranked model includes the parameters persistence probability (*PER, which is 1 – extinction probability*), duration of persistence (*T*, time horizon), inbreeding depression (*INB*) and catastrophes (*CAT*):

$$\begin{aligned}\mathrm{Ln}(MVP_{st}) = {} & \mathrm{Ln}(MVP_{orig}) + \beta_{\mathrm{PER}} * \mathrm{Ln}(PER_{ST} / PER_{ORIG}) \\ & + \beta_{\mathrm{TH}} * \mathrm{Ln}\,(T_{ST} / T_{ORIG}) + \beta_{INB} * INB + \beta_{CAT} * CAT\end{aligned} \tag{2}$$

where ORIG stands for original, ST for standardized, $\beta_{\mathrm{PER}} = 18.26427$, $\beta_{\mathrm{TH}} = 0.4164041$, $\beta_{\mathrm{INB}} = 0.912271$, $\beta_{\mathrm{CAT}} = 0.5432057$ (Traill, pers. Comm.). *INB* and *CAT* are binary. While Traill *et al*. [10] standardized persistence probability by setting it at 99% and the 'duration of persistence' at 40 generations, we use 95% and 100 years, which are values more common in wildlife studies [15], consistent with earlier work [11,31] and recommended by listing authorities such as IUCN [30]. In cases where Traill *et al.* [10] found multiple MVP estimates (derived from different studies) for one species, we averaged the standardized MVP values. See Appendix A for the original and standardized data. The MAR database and underlying parameters are available online on http://www.globio.info/what-is-globio/new-developments. The meta-analysis of Traill *et al*. [10] includes studies on birds, mammals, fish, reptiles, amphibians, insects, marine invertebrates and plants. We focus on birds and mammals, as these taxa were represented by a relatively large set of species (n=49 and n= 89, respectively out of 212). Moreover, home range and density data quantity and quality tend to be better for these taxa, the MVP and MAR concepts are more easily accepted as applicable, and the scale at which populations operate (square kilometres rather than square meters) is more consistent with the goal of conducting large-scale assessments and the typical input maps (land use/land cover) available to do so.

Towards a standardized individual area requirements dataset

Population density and home range size for bird and mammal species can be derived empirically in different ways, as discussed by e.g. Harris *et al*. [32] and Seaman & Powell [33]. A large bulk of studies is by now available, especially since the development of radio tracking techniques. However, we could only find data for some of the species in the MVP database, and these were highly challenging to standardize due to a range of confining effects (e.g. landscape structure and habitat quality; see also Pe'er *et al*. [17]). In our effort to yield a standardized database, we therefore decided to use an empirical relation between density or home range size and body weight. This relation was found in a number of studies for different species and species groups [20,34-37]. 'Body weight' is in this perspective considered as an independent life trait of a species, and can be easily assessed when adding species to the database.

For mammals, we repeated the analysis by Jetz *et al*. [20], based upon the density data of Damuth [37] because of the large dataset. As different databases list different diets for species, we used the panTHERIA database in case of doubt http://esapubs.org/archive/ecol/E090/184/ [38]. The MAR database and underlying parameters including diet are available online at http://www.globio.info/what-is-globio/new-developments.

For birds, no thorough meta-analysis for this relationship was found. Schoener [39] provided home ranges for 77 bird species. He found significant relations for carnivorous birds and all trophic levels pooled, however not for omnivores and herbivores. In this study we therefore used the relation for pooled trophic levels, after adding more recent home range data for 11 species from literature. See Appendix B for details.

For colony breeders, the very concept of individual area requirements may be problematic, as many colony breeders breed on land but forage in water, using vast areas. Area is usually not the limiting factor here, so the MAR concept is of limited use and Equation (1) is unsuitable. Consequently, we removed 13 out of 49 bird species, and 9 out of 89 mammal species from our database. The removed colony breeders included birds such as penguins, terns and puffins and mammals such as seals, sea lions and manatees.

Calculating MAR

With the standardized data on MVP and estimated home range size (birds) and density (mammals), standardized MAR estimates could be calculated for the selected 80 mammal and 36 bird species using Equation 1. In order to explore the uncertainty, a 95% confidence interval was calculated for the MAR estimates, using the variation in both the MVP dataset (variation between estimates available for the same species) and the individual area requirements dataset (variation in the relation between body weight and individual area requirements). For details of the method, see Appendix C.

Exploring the 'natural area size – fraction of species assumed to meet their minimum area requirements' relationship

By sorting the MAR values of the 80 mammal and 36 bird species, we produced a cumulative graph that shows the relationship between natural area size and the proportion of species of conservation interest potentially protected. In doing so we make the simplifying assumptions that (i) the selected bird and mammal species in this study represent the variation in MAR-values of all bird and mammal species of interest, and (ii) the MAR is unaffected by other threats than habitat loss. Confidence intervals of the individual MAR-values were calculated according to the method outlined in Appendix C.

In order to explore the robustness of the relationship, we look separately at birds and mammals as well as the combination of the two.

There are reasons to assume that the relation between area and this biodiversity proxy is different for different biomes, with different resource concentrations per unit area and different species assemblages in productive regions such as rainforests versus deserts and arctic areas. We perform separate analyses for different biomes and continents. Of the 116 species in our database, we found sufficient species occurring in North and Central America (n=45) enabling comparison over four widespread biomes: 'tundra' (22), 'boreal forest' (27), 'temperate mixed forest'

(22) and ‘grassland/steppe’ (21). There is an overlap due to species occurring in more than one biome.

From MAR to global biodiversity assessment

To illustrate the use of MAR in a global biodiversity assessment we applied the combined MAR curve at a global level for both the current situation and a future projection. For the current situation patches of natural habitat were derived from an overlay of a land cover land use map with a map of the main roads. A future projection was constructed by including expected land use change and expected change of the road system.

The GLC2000 global land cover data set [40] with a resolution of 30 arc seconds (approximately 1 by 1 km) was used to calculate patch sizes by first reclassifying the GLC2000 Global Land Cover data into two classes: man-dominated land (including croplands and urban areas) and natural land (the remaining terrestrial area). Adjacent cells of natural land were grouped together into patches using ArcGIS software [41] resulting in separate semi-polygons, ignoring metapopulation structure. We thus make the simplifying assumption that completely converted land is not suitable for any of the relevant species and that the remainder is potentially suitable land. Potentially suitable land includes all protected and non-protected forests and other vegetation, such as the vast areas of grasslands that are used for livestock grazing. We therefore underestimate the suitability of croplands and urban areas for biodiversity and overestimate the suitability of used grassland and used forests for biodiversity.

An overlay with the main roads resulted in a map of patches and their sizes of natural areas. The main roads are derived from an extension to the well-known and still commonly used Vector Map of the World (VMAP), a later version of the Digital Chart of the World [42]. This infrastructure dataset only captures about 30% of the current road network [43] [44] [45]. The extension is based on the Global Roads Inventory Project [46,47], aiming at creating a new global roads database suitable for global assessments. On a country-by-country basis geospatial road network data were collected from almost 60 different sources ranging from United Nations organizations, national spatial data infrastructures (NSDI’s), national mapping agencies, NGO’s, universities and the OpenStreetMap project. The United Nations UNSDI-Transportation data model was applied to the collected datasets to create a consistent and transparent global roads database. This data model was developed by the Logistics Cluster of the UN World Food Programme [48]. The GRIP database distinguishes four categories of roads: highways, primary roads, secondary roads and tertiary roads. We assume that currently highways, primary and secondary roads may have a separating effect on natural areas and these categories were included in calculating patch sizes.

The land use change projection is derived from the IMAGE 2.4 model [49] using the OECD baseline scenario, which is a trend scenario that assumes minor changes in current policies but includes policy actions agreed upon in different international conventions [50]. Land use change is projected with a resolution 0.5 by 0.5 degrees. Therefore we first assigned the patches to grid cells of 0.5 by 0.5 degrees, so that one grid cell may contain no patch, one or more single patches and/or a part of a larger patch. To each grid cell we attributed two different variables: the size of the total patch and the size of the patch within the cell. This is repeated for every patch within the grid cell. Future patch sizes were adapted as a result of the projected land-use change, by adding or subtracting the amount of natural area assigned to each grid cell. A future road map was constructed by upgrading tertiary roads to secondary or primary roads. The result was used for calculating the new patches. Values from the MAR curve were attributed to each patch and average values per grid-cell were calculated as an area weighted average [26]. Other GLOBIO3 applications take several habitat quality variables into account [25,26], but for the sake of simplicity, we ignore habitat quality here.

Results

The results of applying Equations 1 and 2 to the database of selected bird and mammal species are shown in Table 1 and 2, giving specific MAR estimates and the 95% range. If more than one estimate was available for a species we used the average (see Appendix A for original estimates). Using the median value instead of the average did not make much difference overall. Appendix B and C summarize the relation between body weight and density or home range size. Adding bird data of 11 additional species only slightly changed the original relation and improved the goodness of fit (r^2 increased from 0.60 to 0.65, see Appendix B for details).

Figure 1 depicts the MAR estimates for the 80 mammal species and 36 birds, relating size of a natural area to the fraction of mammal species with a viable population that could fit in this area, under the assumptions listed above. One species, the Greater white toothed shrew (*Crocidura russula*), has a relatively large confidence interval, resulting from multiplying a high MVP value (4747) with a low estimated area requirement (0.0053 km^2) for the smallest animal (estimated bwt = 10 gram) in the data set.

Figure 2A shows the results of an analysis across biomes for North American species, comparing the original line based on all 116 species (as in Figure 1C) with the lines for the separate biomes. The North-and Central-American biome lines have a relatively large fraction of high-MAR species; out of the top 10 of species with the highest MAR

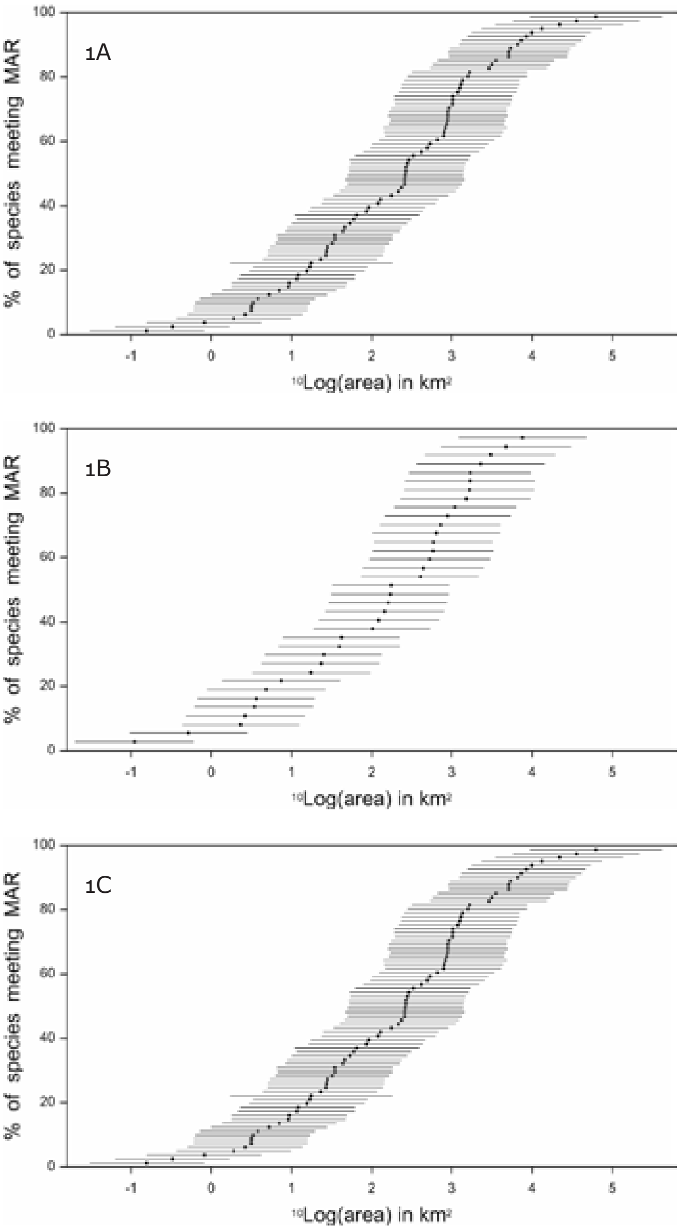

Figure 1. Fraction of mammal (A: n=80), bird (B: n=36) and mammal and bird (C: n = 116) species assumed to meet their minimum area requirements (a proxy for ecosystem integrity), as a function of the size of a natural area. The graphs include a 95% confidence interval (see Appendix C)

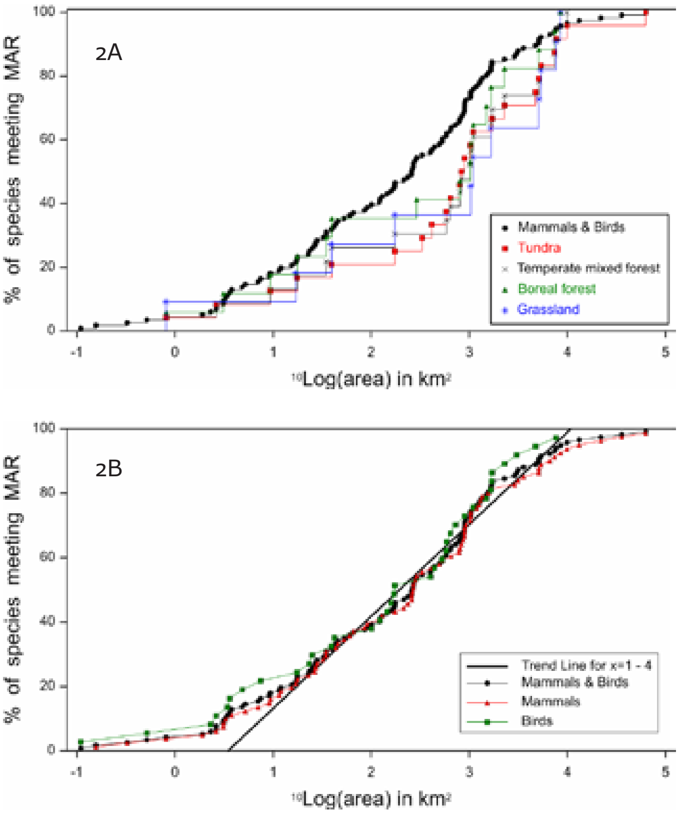

Figure 2. (A) Fraction of species assumed to meet their minimum area requirements (a proxy for ecosystem integrity) as a function of the size of a natural area, for different biomes: comparing the original line based on all 116 species, with the lines for four separate biomes of North and Central America with large areas and substantial numbers of species. The relations for separate biomes do not significantly differ from a random sample from the complete data set. (B) adding a trend line calculated for values of x between 1 and 5 suggesting a rule of thumb where the fraction of species assumed to meet their minimum area requirements (a proxy for ecosystem integrity) in areas between 10 km^2 (LOG10= 1) and 10 000 km^2 (LOG10= 4)' equals Y=-15.45 + 28.607 LOG(AREA).*

in the database, six occur in North-America (Polar bear, Wolverine, Bobcat, Golden eagle, Grizzly bear, Cougar).

In the absence of data to cross-compare all continents and biomes, we fitted a regression line through the core of the graph suggesting a possible rule of thumb where the fraction of species that can have a MVP in areas between 10 km^2 (LOG^{10}= 1) and 10 000 km^2 (LOG^{10}= 4)' equals Y=-15.45 + 28.61* LOG(AREA) (Figure 2B).

Figure 3 shows the estimated fraction of mammal and bird species of conservation interest that may not have viable populations already in the year 2000 (A) and the fraction expected to be unviable in 2050 (B) under land use change according to OECD baseline scenario, assuming that current tertiary roads would be upgraded to secondary or primary roads and become a barrier to wildlife. The maps reveal large regions of the world, namely those characterized by high urbanisation and agricultural activities, where even in 2000 the available area of unfragmented natural habitats may be insufficient for sustaining viable populations of a large fraction of mammal and bird species, even if these species may still occur in these regions. Between 2000 and 2050 further

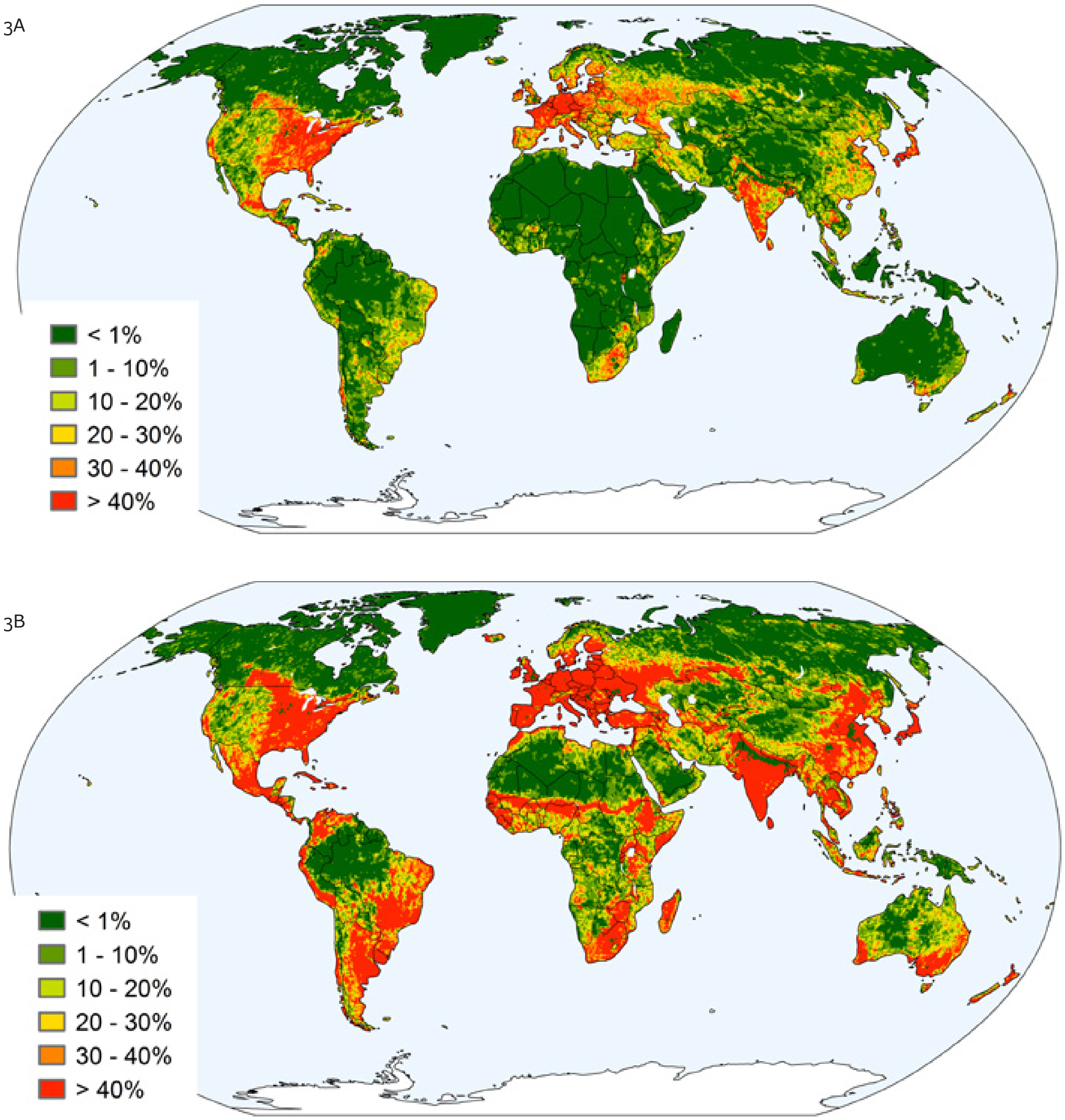

Figure 3. Application of the results to a land use/land cover map from 2000 (A) and the expected scenario in 2050(B). The figure shows the average loss of biodiversity due to fragmentation. See [25,26] for details of the methods.

parts of the world are anticipated to diminish in terms of their capacity to support the area requirements of species, whereas locally conditions may improve because of land abandonment. Particular regions of pressure emerging from this analysis are the sub-tropical regions of South America and Africa, areas of rapid human expansion in Eastern Asia, but also Eastern Europe and Central America.

Discussion

Main conclusions

Deciding how much habitat is needed to achieve long-term conservation goals requires robust rules of thumb because in many situations there is insufficient data to develop a species-specific MAR analysis for a range of relevant species. This paper proposes a method for constructing a MAR database from an MVP database, making it possible

Table 1. Minimum Area Requirements (MAR) in km^2 for terrestrial mammal species, including underlying parameter values: trophic level (food), standardized MVP estimate, bodyweight (g) (BWT) and estimated individual area requirements (IAR) (km^2). 95% confidence interval is indicated by MAR-min and MAR-max. See text for full explanation and Appendix C for calculation. Species are sorted for their MAR-value.

Genus	Species	Common name	Food	MVP estimate	BWT estimate	IAR estimate	MAR estimate	MAR min	MAR max
Burramys	parvus	Pygmy possum	Omnivore	72.66	50	0.003	0.22	0.03	0.81
Petauroides	volans	Marsupial glider	Herbivore	39.39	1300	0.012	0.46	0.06	1.69
Peromyscus	Maniculatus	Deer mice	Omnivore	669.06	24	0.002	1.15	0.16	4.26
Saimiri	oerstedii citrinellus	Costa Rica squirrel monkey	Omnivore	102.31	800	0.026	2.69	0.37	9.83
Petaurus	gracilis	Mahogany glider	Omnivore	270.51	350	0.014	3.74	0.51	13.65
Sciurus	niger	Fox squirrel	Herbivore	573.27	750	0.008	4.40	0.60	16.09
Gymnobelideus	leadbeateri	Leadbeater’s possum	Omnivore	536.90	180	0.008	4.42	0.61	16.17
Hylobates	moloch	Javan Gibbon	Omnivore	39.52	5500	0.118	4.64	0.63	17.20
Hylobates	lar	Lar gibbon	Omnivore	39.86	6530	0.134	5.35	0.72	19.86
Macaca	silenus	Lion tailed macaque	Omnivore	49.56	7500	0.150	7.41	1.00	27.54
Trichosurus	caninus	Brushtail possum	Herbivore	780.21	1450	0.013	9.95	1.36	36.34
Marmota	marmota	Alpine marmot	Herbivore	364.35	5500	0.036	12.97	1.78	47.37
Dama	dama	Fallow deer	Herbivore	52.47	70000	0.252	13.23	1.79	48.78
Pan	troglodytes	Chimpanzee	Omnivore	29.31	41000	0.560	16.42	2.16	62.43
Dipodomys	stephensi	Kangaroo rat	Herbivore	14550.60	65	0.001	17.02	2.30	62.84
Zyzomys	palatalis	Carpentarian rock rat	Herbivore	24955.72	45	0.001	21.99	2.97	81.41
Antilocapra	americana sonoriensis	Pronghorn	Herbivore	118.95	53000	0.204	24.21	3.29	89.13
Crocidura	russula	Greater white toothed shrew	Carnivore	4746.92	10	0.005	25.01	1.71	182.47
Rhinopithecus	brelichi	Guizhou snub-nosed monkey	Herbivore	515.40	11500	0.063	32.37	4.42	118.39
Urocyon	littoralis	Island grey fox	Omnivore	373.50	4500	0.101	37.56	5.08	138.85
Dicerorhinus	sumatrensis	Sumatran rhino	Herbivore	20.48	950000	1.876	38.43	5.10	144.79
Ozotoceros	bezoarticus	Pampas deer	Herbivore	268.45	35000	0.148	39.70	5.40	145.85
Leontopithecus	rosalia	Golden lion tamarin	Omnivore	2154.60	609	0.021	45.78	6.26	167.37
Ovis	canadensis	Bighorn sheep	Herbivore	173.08	81940	0.285	49.26	6.67	181.82
Equus	zebra	Cape mountain zebra	Herbivore	67.25	280000	0.733	49.29	6.62	183.56
Trinomys	eliasi	Atlantic forest spiny rat	Herbivore	11907.61	450	0.005	61.74	8.44	225.89
Petaurus	australis	Aus gliding marsupial	Omnivore	3214.89	570	0.020	64.89	8.88	237.19
Brachyteles	arachnoides	Muriqui	Omnivore	318.40	13500	0.236	75.21	10.05	281.38
Capra	hircus	goat	Herbivore	520.87	40000	0.164	85.37	11.61	313.82
Mustela	nigripes	Black-footed ferret	Carnivore	359.47	885	0.258	92.85	11.06	389.65
Phascolarctos	cinereus	Koala	Herbivore	3659.94	5000	0.033	121.07	16.58	442.09
Castor	fiber	Eurasian beaver	Herbivore	1143.86	24500	0.112	128.56	17.53	471.51
Marmota	flaviventris	Yellow bellied marmot	Herbivore	6833.97	3500	0.025	171.79	23.53	627.10
Bubalus	mindorensis	Tamaraw	Herbivore	293.96	227500	0.625	183.60	24.69	682.65
Aepyceros	melampus	Impala	Herbivore	1236.48	52000	0.201	248.01	33.69	912.92
Equus	caballus przewalskii	Przewalski’s horse	Herbivore	348.60	350000	0.870	303.33	40.64	1131.91
Lagorchestes	conspicillatus	Spectacled hare wallaby	Herbivore	16797.45	2590	0.020	334.91	45.88	1222.40
Macropus	robustus	Euro	Herbivore	3023.54	26875	0.121	364.91	49.73	1338.86
Neofelis	nebulosa	Clouded leopard	Carnivore	77.73	25000	4.699	365.25	46.82	1424.86

Genus	Species	Common name	Food	MVP estimate	BWT estimate	IAR estimate	MAR estimate	MAR min	MAR max
Meles	meles	Eurasian badger	Omnivore	2000.37	9926	0.186	372.04	49.91	1386.72
Ovis	aries	Mouflon	Herbivore	2900.41	30000	0.131	380.97	51.89	1398.48
Tapirus	bairdii	Baird's Tapir	Herbivore	470.24	320000	0.812	381.90	51.21	1424.01
Ailuropoda	melanoleuca	Giant panda	Herbivore	1176.46	102000	0.337	396.33	53.61	1464.85
Canis	rufus	Red wolf	Carnivore	78.06	28500	5.265	411.00	52.45	1610.40
Rangifer	tarandus	Arctic Island caribou	Herbivore	979.14	160000	0.476	466.44	62.90	1729.52
Ovibos	moschatus	Muskox	Herbivore	799.68	280000	0.733	586.03	78.67	2182.63
Phacochoerus	aethiopicus	Warthog	Herbivore	2396.08	85000	0.293	701.52	95.01	2589.77
Papio	cynocephalus	Chacma Baboon	Omnivore	2615.99	17500	0.289	756.00	100.68	2838.29
Cercopithecus	aethiops	Vervet monkey	Omnivore	9203.18	4500	0.101	925.52	125.18	3421.43
Bison	bonasus	European bison	Herbivore	591.18	950000	1.876	1109.33	147.21	4179.90
Ursus	americanus	Black bear	Omnivore	638.36	180000	1.769	1129.01	144.34	4415.38
Martes	americana	American marten	Carnivore	4325.63	936	0.271	1173.04	140.33	4902.72
Cervus	eldii	Elds deer	Herbivore	3676.45	100000	0.332	1219.79	165.03	4507.86
Ovis	dalli dalli	Dall's sheep	Herbivore	4785.45	74000	0.263	1259.32	170.71	4645.00
Canis	simensis	Ethiopian wolf	Carnivore	211.68	33000	5.980	1265.82	160.63	4987.59
Babyrousa	babyrussa	Barbirusa	Omnivore	1469.74	71500	0.863	1268.31	165.15	4870.33
Hippotragus	equinus	Roan antelope	Herbivore	2308.65	200000	0.566	1305.86	175.79	4850.29
Cervus	elaphus	Elk	Herbivore	1943.87	286000	0.745	1447.96	194.35	5393.83
Elephas	maximas	Asian elephant	Herbivore	245.30	4250000	5.944	1458.16	190.10	5592.36
Sus	scrofa	Wild boar	Omnivore	1400.16	91483	1.045	1463.38	189.67	5645.36
Gorilla	gorilla	Mountain gorilla	Omnivore	1219.95	130000	1.373	1675.44	215.66	6508.30
Rhinoceros	unicornis	Indian one-horned rhinoceros	Herbivore	590.71	1750000	3.003	1773.80	233.79	6728.96
Ursus	thibetanus japonicus	Japanese black bear	Omnivore	1635.74	100000	1.120	1832.06	237.04	7079.79
Cercocebus	galeritus galeritus	Tana River crested Mangabey	Omnivore	13829.89	6750	0.138	1906.05	256.78	7074.11
Lycaon	pictus	African wild dog	Carnivore	435.02	27500	5.104	2220.53	283.71	8689.71
Odocoileus	virginianus	White-tailed or key deer	Herbivore	7095.40	100000	0.332	2354.15	318.51	8699.99
Rhinoceros	sondaicus	Javan rhinoceros	Herbivore	1574.45	1450000	2.598	4090.79	540.34	15485.19
Loxodonta	africana	African elephant	Herbivore	713.51	4500000	6.212	4432.12	577.39	17010.92
Diceros	bicornis	Black rhinoceros	Herbivore	2399.84	1102000	2.104	5048.15	668.82	19051.38
Lynx	lynx	Lynx	Carnivore	1861.32	20000	3.871	7205.84	929.39	27934.49
Canis	lupus	Wolf	Carnivore	921.70	45000	7.828	7215.16	902.85	28830.07
Felis	concolor	Cougar	Carnivore	949.38	46000	7.979	7575.01	946.83	30301.40
Bos	taurus	Vorderwald	Herbivore	5544.84	825000	1.683	9334.14	1240.45	35118.95
Ursus	arctos horribilis	Grizzly bear	Omnivore	3173.98	400000	3.290	10441.77	1311.21	41576.34
Lynx	rufus	Bobcat	Carnivore	3396.29	18000	3.533	11998.77	1551.30	46403.27
Gulo	gulo	Wolverine	Carnivore	2780.07	27000	5.024	13966.43	1785.59	54621.03
Acinonyx	jubatus	Cheetah	Carnivore	2314.38	46600	8.069	18675.23	2332.76	74753.39
Panthera	tigris	Tiger	Carnivore	1159.86	185000	26.714	30984.87	3509.95	136763.14
Panthera	leo	Lion	Carnivore	2109.57	163353	23.978	50584.06	5793.34	220835.27
Ursus	maritimus	Polar bear	Carnivore	1750.16	388000	50.820	88943.22	9363.49	422433.11

Table 2. Minimum Area Requirements (MAR) in km^2 for terrestrial bird species, including underlying parameter values: standardized MVP estimate, trophic level, bodyweight (g) and home range size (ha). 95% confidence interval is indicated by MAR-min and MAR-max. See text for full explanation and Appendix C for calculation. Species are sorted for their MAR-value.

Genus	Species	Common name	MVP	BWT	Homerange	MAR estimate	MAR min	MAR max
Hirundo	atrocaerulea	Blue swallow	50	13	0.62	0.15	0.02	0.60
Parus	major	Great tit	157	18	0.93	0.73	0.10	2.82
Lichenostomus	melanops cassidix	Helmeted honeyeater	330	32	1.99	3.28	0.43	12.47
Parus	atricapillus	Black capped chickadee	1410	12	0.53	3.73	0.48	14.58
Zosterops	lateralis chlorocephala	Capricorn silvereye	1911	11	0.51	4.83	0.62	18.91
Mohoua	ochrocephala	Mohua	629	28	1.63	5.13	0.67	19.55
Dendroica	kirtlandii	Kirtland's warbler	2035	14	0.67	6.83	0.88	26.53
Ficedula	hypoleuca	Pied flycatcher	3149	14	0.67	10.53	1.36	40.87
Melospiza	melodia	Song sparrow	4647	20	1.07	24.86	3.24	95.43
Delichon	urbica	House martin	5974	20	1.10	32.89	4.29	126.19
Lichenostomus	melanops	Yellow tufted honeyeater	3560	32	1.99	35.46	4.67	134.64
Buteo	jamaicensis	Red-tailed hawk	57	1120	194.29	55.71	6.85	226.44
Picoides	borealis	Red cockaded woodpecker	3581	48	3.32	59.38	7.86	224.29
Aphelocoma	coerulescens	Florida scrub jay	4669	77	6.12	142.97	18.96	538.90
Tetrax	tetrax	Little bustard	285	782	122.20	173.95	21.79	694.18
Gallirallus	sylvestris	Lord Howe Island woodhen	604	496	67.82	204.88	26.18	801.59
Rostrhamus	sociabilis	Snail kite	878	402	51.68	226.88	29.22	880.78
Accipiter	nisus	Sparrowhawk	1850	238	26.19	242.23	31.68	925.90
Certhia	americana	Brown creeper	32188	26	1.54	247.11	32.41	942.10
Amazona	vittata	Puerto Rican parrot	4061	250	27.98	568.21	74.23	2174.72
Falco	peregrinus anatum	American peregrine falcon	841	908	148.06	622.87	77.47	2503.93
Nestor	notabilis	Kea	1073	868	139.68	749.54	93.44	3006.34
Tympanuchus	phasianellus	Sharp-tailed grouse	1147	885	143.33	821.96	102.36	3300.09
Nestor	meridionalis	Kaka	2945	429	56.23	828.03	106.40	3222.04
Grus	canadensis	Sandhill crane	156	4472	1162.88	905.91	101.59	4038.99
Strix	uralensis	Ural owl	1668	785	122.66	1023.03	128.16	4083.15
Tetrao	urogallus	Capercaillie	371	2950	679.29	1259.74	145.75	5443.93
Bubo	virginianus	Great horned owl	1443	1210	214.80	1549.65	189.81	6325.99
Meleagris	gallopavo	Wild turkey	246	6050	1718.55	2110.56	230.99	9642.32
Grus	antigone	Eastern sarus crane	268	6163	1760.14	2354.79	257.32	10774.67
Gypaetus	barbatus	Bearded vulture	294	5800	1627.34	2391.62	262.66	10888.26
Tetrao	tetrix	Black grouse	2581	1083	185.95	2399.98	295.77	9737.25
Haliaeetus	leucocephalus	Bald eagle	514	4740	1253.74	3222.41	359.73	14433.11
Grus	americana	Whooping crane	487	6163	1760.14	4287.57	468.52	19618.41
Cygnus	columbianus	Whistling swan	684	6705	1962.54	6711.96	728.28	30929.54
Aquila	chrysaetos	Golden eagle	1977	4264	1093.32	10808.79	1216.68	48011.64

to assess land use change scenarios and produce policy relevant maps. We implement this method for birds and mammals, to derive a relationship between the size of a natural area and the fraction of conservation priority species assumed to meet their minimum area requirements -a proxy for ecosystem integrity [24], and demonstrate the results of applying these relations to global maps. Naturally many uncertainties are associated with such maps, and therefore they must be seen as a tool for communication on the science-policy interface, and directing future research, rather than depicting the result of highly credible, quantitative assessments [51-53].

We believe that despite the limitations and caveats, this simple and transparent method has the merits of allowing identification of general patterns and differences between scenarios on the global or continental scale [53]. A comparison of the resulting map for the year 2000 (Figure 3A) to published maps of biodiversity hotspot or other areas of conservation importance [54-56], indicates that some of the known hotspots are indeed shown as being under threat due to fragmentation. Such regions include the Caucasus, Cape region, the Atlantic Rainforest and many other coastal zones where human density is high. It also highlights areas such as the Indian subcontinent, Japan and southern Africa, where fragmentation may be underestimated by current approaches – yet with the caution that our analysis only takes into account birds and mammals, and is therefore potentially biased towards large, area-demanding species.

Note however that fragmentation may equally affect plants or invertebrates and eventually take its toll [6]. Even more importantly, when comparing the projected map for 2050 based on land use change trends and “upgrading” roads and hence assuming increased fragmentation (Figure 3A), this reveals a very broad range of pressure-areas, many of which coincide with the biodiversity hotspots – e.g. in Western South America or Brazil’s Cerrado. The identified threatened areas extend however far beyond these hotspot areas, and indicate a particularly alarming belt of frontier areas in Africa (Sahel, Eastern Africa) and South-Eastern Asia. Thus, even if the map is based on a range of simplifying assumptions, it already indicates a need to increase conservation attention at peri-urban, subtropical and temperate regions where urbanization and fragmentation processes are currently rapidly ongoing.

Our results suggest that many existing nature areas may be too small for long term viability of the large mammal and bird species that occur there. This conclusion is not new [16,18,57,58]. Although some assumptions may lead to over pessimistic results, there is no reason for optimism in light of climate change and other threats which exert additional pressures not accounted for. One may even argue that the map is in fact optimistic: we actually assume that all “undisturbed” habitats are suitable for all species, whereas in reality many are not and hence the actual status for many species is likely to be even worse. Populations well below MVP can be aided to survive in ecological networks (metapopulations) and/or by active management such as assisted migration (inbreeding prevention) and protective measures against sudden drops due to extreme events: feeding in times of food shortage, predator management or vaccination against disease.

Merits of the method

The main merit of the exercise may lay in the capacity to reveal spatial patterns of human-wildlife conflict, patterns that are expected to be quite robust in the light of limitations and uncertainties of the method [51,53]. Quantitative dose-response relations between pressures and biodiversity indicators are required for assessing the effectiveness of (i) international agreements and policies such as REDD+ [59], (ii) targets to reduce pressures such as the Aichi targets [2] as well as (iii) national policies. Using a biodiversity indicator - such as fraction of species assumed to meet their minimum area requirements - which is 100% for vast, pristine environments and drops as human pressures rise, makes this approach comparable and compatible with other approaches and indicator frameworks working with ‘species richness of original species’ or ‘fraction of remaining species’ [60]. These indicators can then easily be combined into a multi-stress biodiversity indicator framework because they use a common currency.

Alternative methods to link area to a biodiversity index such as the SAR - Species Area Relationship approach [21-23], are not taking long-term population viability into account, therefore the long-term perspective is missing. More-over, they do not yield a biodiversity index between 0 (completely devastated areas) and 1 (completely pristine areas) as the value keeps rising with increasing area, which makes it difficult to combine it together with other biodiversity indicators due to the lack of a common currency.

The relation developed in this paper is therefore better than SAR for numerous applications. It has been implemented in the GLOBIO-model and can be used by others for modelling the quantitative aspects of the impact of habitat loss and large scale fragmentation on the fraction of original species, while taking into account long-term perspectives.

Limitations and outlook

MAR estimates cannot easily be validated empirically for at least two reasons. First, one would need data on population persistence/extinction for long periods of time – because of the 100 year time horizon. Second, many replicas would be needed – because of the probabilistic nature, i.e. with 5% extinction risk. Moreover, all other conditions should remain constant.

Various caveats can be listed for the MAR approach in general and our study in particular. Here, we therefore review the limitations, providing ideas and guidelines on how to resolve them en route to an improved assessment of species' needs and, with it, enhanced applicability of the approach.

(1) The study focuses only on a selection of birds and mammals, with an overrepresentation of large, charismatic species. Traill *et al*. [10] state that although 85.3% of mammals in their database exceed 1000 g, by contrast, only 31% of 4049 extant mammals listed in a large database of body masses are over 1000 g. Figures 1, 2 and 3 would look differently if a more representative set of species were included. On the other hand, many small mammals and birds are a poor biodiversity indicator because they occur in man-dominated agricultural and urban areas as well as in natural areas. Our database now contains mainly conservation priority species. This caveat can be remedied by adding species of interest for a particular policy problem, and/or selecting a representative set of species for a certain region or biome – if relevant data are available.

(2) To illustrate the method we used all species of all continents and biomes together, although differences between biomes exist in species richness as well as in resource availability [16,61,62]. However there are no simple rules of thumb here; Pe'er *et al*. [17], attempting to explain MAR's with ecological and environmental variables, surprisingly found evidence for increasing MAR values with temperature or precipitation. In this study, not enough data were available to test for differences. The results as shown in Figure 2A suggest that differences between biomes and/or continents might exist, but the sample sizes are too small to derive conclusions based upon these results. North-American MVP studies seem to be mainly focused on large carnivore species. Our method can be easily applied to specific biomes or continents using data only on species belonging to a region of interest. The problem of representativeness is demonstrated in small islands. Many islands worldwide are not large enough for minimum viable populations of large animals, according to our database, and indeed, many island ecosystems are not inhabited by, e.g., large carnivores. However, it would be absurd to conclude that all islands of less than 100 000 km^2, in their pristine state, lack ecosystem integrity, because they cannot secure long-term viability of large carnivores. The MAR dataset in the present form therefore doesn't seem fit for small islands.

(3) Our current approach does not take into account vegetation structure, habitat heterogeneity and habitat quality factors such as degradation, pollution, disturbance, hunting, logging or edge effects. We assume that "suitability" is binary and equal for all species. This introduces a bias. Arguably, more detailed information of area requirements versus availability may not alter the qualitative outcome of a comparison between current and future scenarios, as the same biases can be assumed to affect both maps equally [53]. But it seems that the maps, as of the information used so far, cannot identify intensification process which may enhance biodiversity loss without leading to land cover change. The bias can be compensated by including other stress factors in a more complex model such as GLOBIO3 [25,26] on a global/continental scale. GLOBIO is built upon a series of dose-response relationship linking environmental change to the relative Mean Species Abundance (MSA), a measure for ecosystem integrity [26]. Drivers and pressures included are, apart from habitat loss and fragmentation: land use change (including forestry) and land use intensity, climate change, N-deposition, impacts of infrastructure. Since 2005 about 20 countries across the world used GLOBIO for more or less extensive national and sub-regional biodiversity assessments [51,63]. For application on a local, landscape scale we recommend using more detailed methods such as landscape cohesion assessment [64] or Conefor [65].

(4) Ignoring metapopulation dynamics and regarding natural areas as islands in a sea of unsuitable habitat introduces yet another bias. In metapopulations, a certain extinction risk of local populations is acceptable, if re-colonization from neighbouring areas can occur. Our binary approach, where habitat is either regarded as continuous or completely disconnected, simplifies real spatial dynamics leading to either overestimation of biodiversity, when fragmentation is present on a scale not detectable by us (i.e. within cells of 1 square km), or underestimation, when patches that in fact exchange dispersers are regarded as isolated. The difference between Figure 3A and 3B is mainly due to the assumption that roads of a certain type act as absolute barriers, which may be true for some species, but certainly not for all. Again, we propose to use other methods on a landscape level whenever metapopulation dynamics are considered important.

There are several conceptual improvements possible. Although there should be little discussion about Equation 1, the two components of the MAR need attention. Not being able to validate the data empirically (see 4.1), the outliers in the original database (Appendix A) need to be scrutinized and possibly omitted. For further discussion on the use of MVP's and MAR's see Pe'er *et al*. [30] [17]. The individual area requirements component on the other hand can easily be validated. We now used simple formulas based upon body weight (birds, mammals) and trophic level (mammals), the estimated areas from these models can easily be replaced by more realistic ones, possibly region and/or biome specific.

The tool needs to have better visibility among the research and policy making community in order that it can be further discussed, used and developed. Thus, as a final recommendation, we propose that our database (available online at http://www.globio.info/what-is-globio/new-developments) is used in two ways. First, as a step forward for building a comprehensive MAR database with which scientists or policy makers can tackle specific problems, assessing how much habitat is needed to achieve long term conservation goals. Second, as the basis for assessing nature policy and land use/land cover change scenarios for their impacts, in global assessments. In the light of the uncertainties, the resulting biodiversity assessments can well serve as a tool for communication on the science-policy interface.

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Appendix A. MVP estimates for the mammal species used in this study

Traill et al. (2007) standardized MVP estimates as provided by the original studies, correcting for the parameters 'persistence probability (99%), duration of persistence (40 generations), inbreeding depression and catastrophes' and including a phylogenetic correction. For this study we adjusted their standardization formula with different parameter values for persistence probability (95%) and duration of persistence (100 years), consistent with Verboom et al. (2001). Means were calculated for each species.

Genus	Species	Common name	MVP estimate from original study	Standardized MVP by Traill *et al.* (2007)	Standardized MVP by authors
Acinonyx	*jubatus*	Cheetah	4036	4036	2205
Acinonyx	*jubatus*	Cheetah	2500	4438	2424
Aepyceros	*melampus*	Impala	2123	2123	1236
Ailuropoda	*melanoleuca*	Giant panda	6224	6224	2196
Ailuropoda	*melanoleuca*	Giant panda	215	446	157
Antilocapra	*americana peninsularis*	Peninsular pronghorn	100	68	39
Antilocapra	*americana sonoriensis*	Sonoran pronghorn	150	341	199
Babyrousa	*babyrussa*	Barbirusa	1500	2524	1470
Bison	*bonasus*	European Bison	263	408	178
Bison	*bonasus*	European Bison	1000	2301	1004
Bos	*taurus*	Vorderwald	3301	8041	5545
Brachyteles	*arachnoides*	Muriqui	51	141	50
Brachyteles	*arachnoides*	Southern muriqui	1664	1664	587
Bubalus	*mindorensis*	Tamaraw	175	759	294
Burramys	*parvus*	Pygmy possum	36	105	73
Canis	*lupus*	Wolf	500	1981	864
Canis	*lupus*	Wolf	400	920	402
Canis	*lupus*	Grey wolf	6332	6332	2763
Canis	*lupus*	Gray wolf	100	244	168
Canis	*rufus*	Red wolf	80	151	78
Canis	*simensis*	Ethiopian wolf	150	307	212
Canis	*lupus*	Wolf	40	796	411
Capra	*hircus*	goat	566	566	521
Castor	*fiber*	European beaver	60	546	257
Castor	*fiber*	Eurasian beaver	42	35	16
Castor	*fiber*	Eurasian beaver	1880	4580	3158
Cercocebus	*galeritus galeritus*	Tana River crested Mangabey	8000	31691	13830
Cercopithecus	*aethiops*	Vervet monkey	19547	19547	9203
Cervus	*elaphus*	Elk	5768	5768	3528
Cervus	*elaphus*	Elk	214	521	359
Cervus	*eldii*	Eld's deer	3326	3326	1612
Cervus	*eldii*	Elds deer	76	138	67
Cervus	*eldii thamin*	Thamin (Eld's deer sub sp)	19298	19298	9351
Crocidura	*russula*	Greater white toothed shrew	3865	3865	4747
Dama	*dama*	Fallow deer	26	136	52
Dicerorhinus	*sumatrensis*	Sumatran rhino	25	63	20
Diceros	*bicornis*	Black rhinoceros	6199	6199	2400
Dipodomys	*stephensi*	Kangaroo rat	13355	13355	14551
Dugong	*dugon*	Dugong	28705	48090	12712
Elephas	*maximas*	Asian elephant	25	722	107
Elephas	*maximas*	Asian elephant	25	287	43
Elephas	*maximas*	Asian elephant	40	866	128
Elephas	*maximas*	Asiatic elephant	4737	4737	703
Enhydra	*lutris*	Sea otter	7623	7623	2951
Enhydra	*lutris*	Sea otter	2650	9454	3660
Equus	*caballus przewalskii*	Przewalski's horse	140	675	349

Genus	Species	Common name	MVP estimate from original study	Standardized MVP by Traill *et al.* (2007)	Standardized MVP by authors
Equus	*zebra*	Cape mountain zebra	30	130	67
Eumetopias	*jubatus*	Stellar sea lion	4204	4204	1835
Felis	*concolor*	Mountain lion	5162	5162	2667
Felis	*concolor*	Cougar	20	55	28
Felis	*concolor*	Florida panther	76	262	153
Gorilla	*gorilla*	Mountain gorilla	320	1076	312
Gorilla	*gorilla*	Virunga gorilla	254	619	427
Gorilla	*gorilla beringei*	Mountain gorilla	1000	2356	684
Gorilla	*gorilla beringei*	Mountain gorilla	11919	11919	3457
Gulo	*gulo*	Wolverine	10612	10612	5483
Gulo	*gulo*	Scandinavian wolverine	46	112	77
Gymnobelideus	*leadbeateri*	Leadbeater's possum	200	1039	537
Halichoerus	*grypus*	Grey seal	19165	19165	7419
Hippotragus	*equinus*	Roan antelope	5037	5037	2309
Hylobates	*lar*	Lar gibbon	100	137	40
Hylobates	*moloch*	Javan Gibbon	100	129	40
Lagorchestes	*conspicillatus*	Spectacled hare wallaby	10000	24360	16797
Leontopithecus	*rosalia*	Golden lion tamarin	6587	6587	3836
Leontopithecus	*rosalia*	Golden lion tamarin	1000	812	473
Loxodonta	*africana*	African elephant	1000	2353	576
Loxodonta	*africana*	African elephant	5474	5474	1341
Loxodonta	*africana*	African elephant	500	910	223
Lycaon	*pictus*	African wild dog	20	110	59
Lycaon	*pictus*	African wild dog	100	97	52
Lycaon	*pictus*	African wild dog	2229	2229	1194
Lynx	*lynx*	Eurasian lynx	6563	6563	3658
Lynx	*lynx*	Lynx	15	115	64
Lynx	*rufus*	Bobcat	11079	11079	6453
Lynx	*rufus*	Bobcat	169	584	340
Macaca	*silenus*	Lion tailed macaque	60	140	50
Macropus	*robustus*	Euro	1800	4385	3024
Marmota	*flaviventris*	Yellow bellied marmot	13227	13227	6834
Marmota	*marmota*	Alpine marmot	85	705	364
Martes	*americana*	American marten	6884	6884	4326
Meles	*meles*	Eurasian badger	2901	2901	2000
Mirounga	*angustirostris*	Northern elephant seal	5095	5095	2632
Mirounga	*leonina*	Southern elephant seal	31791	31791	13874
Monachus	*schauinslandi*	Monk seal	340	729	257
Monachus	*schauinslandi*	Hawaiin monk seal	1597	1597	563
Mustela	*nigripes*	Black-footed ferret	214	521	359
Neofelis	*nebulosa*	Clouded leopard	200	178	78
Odocoileus	*virginianus*	White-tailed or key deer	13733	13733	7095
Ovibos	*moschatus*	Muskox	10	32	13
Ovibos	*moschatus*	Muskox	3876	3876	1586
Ovis	*aries*	Mouflon	7334	7334	5057
Ovis	*aries*	Soay sheep	130	1079	744
Ovis	*canadensis*	Bighorn sheep	100	476	224
Ovis	*canadensis mexicana*	Bighorn sheep	12	259	122
Ovis	*dalli dalli*	Dall's sheep	10164	10164	4785
Ozotoceros	*bezoarticus*	Pampas deer	100	520	268
Pan	*troglodytes*	Chimpanzee	25	101	29
Panthera	*leo persica*	Asiatic lion	284	266	109
Panthera	*tigris*	Tiger	119	285	117
Panthera	*leo*	Lion	5792	5792	2370

Genus	Species	Common name	MVP estimate from original study	Standardized MVP by Traill *et al.* (2007)	Standardized MVP by authors
Panthera	*leo persica*	Asian lion	9405	9405	3849
Panthera	*tigris altaica*	Amur tiger	5840	5840	2390
Panthera	*tigris tigris*	Sumatran tiger	2377	2377	973
Papio	*cynocephalus*	Chacma Baboon	7097	7097	2616
Peromyscus	*maniculatus*	Deer mice	1000	460	669
Petauroides	*volans*	Marsupial glider	75	68	39
Petaurus	*australis*	Aus gliding marsupial	750	6222	3215
Petaurus	*gracilis*	Mahogany glider	800	464	271
Phacochoerus	*aethiopicus*	Warthog	4114	4114	2396
Phascolarctos	*cinereus*	Koala	20	393	203
Phascolarctos	*cinereus*	Koala	13774	13774	7117
Phoca	*vitulina*	Harbour seal	50	487	213
Rangifer	*tarandus*	Arctic Island caribou	1000	2218	979
Rhinoceros	*sondaicus*	Javan rhinoceros	8771	8771	3094
Rhinoceros	*sondaicus*	Javan rhinoceros	56	155	55
Rhinoceros	*unicornis*	Indian one-horned rhinoceros	50	157	61
Rhinoceros	*unicornis*	Indian one-horned rhinoceros	2895	2895	1121
Rhinopithecus	*brelichi*	Guizhou snub-nosed monkey	764	1461	515
Saimiri	*oerstedii citrinellus*	Costa Rica squirrel monkey	260	176	102
Sciurus	*niger*	Fox squirrel	285	831	573
Sus	*scrofa*	Wild boar	300	2959	1723
Sus	*scrofa*	Wild boar	1849	1849	1077
Tapirus	*bairdi*	Baird’s Tapir	1200	910	470
Trichechus	*manatus latirostris*	Florida manatee	7044	7044	3074
Trichosurus	*caninus*	Brushtail possum	50	61	27
Trichosurus	*caninus*	Brushtail possum	100	187	81
Trichosurus	*caninus*	Brushtail possum	5116	5116	2233
Trinomys	*eliasi*	Atlantic forest spiny rat	200	1183	920
Trinomys	*eliasi*	Atlantic forest spiny rat	2000	29456	22896
Urocyon	*littoralis*	Island grey fox	150	502	373
Ursus	*americanus*	Black bear	2045	2045	1057
Ursus	*americanus*	Florida black bear	82	319	220
Ursus	*arctos horribilis*	Grizzly bear	250	2547	1112
Ursus	*arctos horribilis*	Grizzly bear	250	1023	446
Ursus	*arctos horribilis*	Grizzly bear	250	851	372
Ursus	*arctos horribilis*	Grizzly bear	250	851	372
Ursus	*arctos horribilis*	Grizzly bear	250	5015	2189
Ursus	*arctos horribilis*	Grizzly bear	101	44743	19526
Ursus	*arctos horribilis*	Grizzly bear	40	395	172
Ursus	*arctos horribilis*	Grizzly bear	3811	3811	1663
Ursus	*arctos horribilis*	Grizzly bear	6221	6221	2715
Ursus	*maritimus*	Polar bear	4961	4961	1750
Ursus	*thibetanus japonicus*	Japanese black bear	100	628	243
Ursus	*thibetanus japonicus*	Japanese black bear	7823	7823	3029
Zyzomys	*palatalis*	Carpentarian rock rat	5400	22905	24956

Appendix B. Bird home range data

In this appendix we describe the steps taken to come to a joint dataset of the Schoener (1968) data with more recent data on bodyweight – area requirement. From this joint dataset we derived the log-linear relationship for birds, as presented in Table 1 of the paper.

Comparing relationship from Schoener data and recent data collected from literature
This serves two purposes: the data used by Schoener might be outdated since his paper dates from 1968. We therefore chose to compare the relationship with more recent area requirement data.. Second, since we use species on the list in Traill et al. (2007) to calculate MAR, we can demonstrate whether the relationship that Schoener found, also applies to these species by collecting area requirements for these specific species. 49 bird species occur on the list in Traill et al. (2007).

As mentioned in the paper, 13 of the 49 species were colony breeders, and as such were excluded. From the remaining 36 species we found area requirement data for 24 species in literature; body weight values were derived from the Birdlife Datazone (Birdlife 2011). The data for these 24 species is presented in Table B1.

Table B1. Data for 24 bird species on the list in Traill et al. (2007).

Species	Weight (g)	Area requirements (ha)	log^{10} weight (g)	log^{10} Area requirements (ha)	Source
Bearded vulture	5800,0	25135,50	3,763	4,400	Brown 1991
Black-capped chickadee	11,6	2,00	1,064	0,301	Smith and Van Buskirk 1988
Black grouse	1082,5	86,08	3,034	1,935	Baines and Hudson 1995, Caizergues 2003, Hoglund and Stohr 1996, Starling 1992
Brown creeper	26,5	15,63	1,422	1,194	Anthony *et al*. 1996, Bock and lynch 1970, Morse 1970
Capercaillie	2950,0	77,71	3,470	1,890	Wegge and Rolstad 1986, Catt *et al*. 1998,
Capricorn silvereye	11,2	0,05	1,049	-1,312	Catterall *et al*. 1982
Florida scrub jay	77,2	11,51	1,887	1,061	Woolfenden and Fitzpatrick 1984+1990
Golden eagle	4263,5	9214,06	3,630	3,964	McGahan 1968. Green 1996, Watson *et al*. 1992
Great horned owl	1210,3	3069,80	3,083	3,487	Minor *et al*. 1993, Hagar 1957
Great tit	18,0	0,64	1,255	-0,193	Drent 1984, Dunn *et al*. 1977. Perrins 1965
House martin	20,5	45,36	1,311	1,657	Cramp and Ward 1934
Kaka	429,0	13,11	2,632	1,118	Greene *et al*. 2010, Preston 2008
Kea	867,5	254,48	2,938	2,406	Bond and Diamond 1992, Elliot and Kemp 1999
Kirtland's warbler	14,0	16,31	1,145	1,213	Probst and Weinrich 1993, Marshall *et al*. 2000, Probst and Weinrich 1986
Little bustard	782,3	71,60	2,893	1,855	Martinez 2000, Wolff *et al*. 2002, Martinez and Tapia 2002, Faria and Rabaca 2004, Garcia de la morena *et al*. 2007
Mohua	27,8	7,02	1,443	0,846	Lawrence 2000
Pied flycatcher	13,9	1,21	1,143	0,083	Virolainen 1984, Alatalo and Lundberg 1981+1984
Red-tailed hawk	1119,9	709,98	3,049	2,851	Johnson 1975, Hagar 1957, Luttich *et al*. 1971, Minor *et al*. 1993, Gates 1972
Sandhill crane	4471,9	52,63	3,650	1,721	Bennett 1989
Sharp-tailed grouse	237,5	398,46	2,376	2,600	Robel *et al*. 1972
Sparrowhawk	237,5	181,82	2,376	2,260	Newton *et al*. 1977
Ural owl	784,5	2000,00	2,895	3,301	Lundberg 1981
Whistling swan	6704,6	807,64	3,826	2,907	Pozdnyakov 2002, Earnst and Rothe 2004, Babcock *et al*. 2002, Wilk 1988
Wild turkey	6050,0	20,00	3,782	1,301	Ellis and Lewis 1967

We linearly regressed the LOG^{10} values of area requirements on the LOG^{10} values of bodyweight following Schoener's analysis (Table B2 of this appendix).
The significance and the "goodness of fit" (r^2) of the literature data analysis are somewhat lower than for the Schoener analysis, however this can be explained by the relatively low number of species. Since the slopes of the two analyses differ only little, we decided to combine the two datasets to create a larger dataset. This joint dataset includes an overlap of four species, for which both values were incorporated.
The results in Table B2 show that the "goodness of fit" of this joint dataset has increased compared to both individual datasets.

Table B2. Analyses of relationship between bodyweight and area requirement of birds for three datasets.

Data set	n	Slope	Intercept	r^2	Pa
Schoener (1968)	75	1.17	-1.50	.60	.001
Literature (as in Table B1)	24	1.00	-0.67	.56	.016
Schoener (1968) +Literature	88	1.19	-1.45	.65	.0001

Appendix C. Estimating uncertainty for MAR data

Variance to mean relationship for MVP data

A plot of ^{10}Log(variance) versus ^{10}Log(mean) for bird and mammal species with replicate estimates of the standardized MVP is given below. Note that the crosses (mammals) and rounds (birds) represent species with replicate estimates, the vertical lines at the bottom of the graph represent the mean MVP estimate for all species (so also for those with only a single replicate).

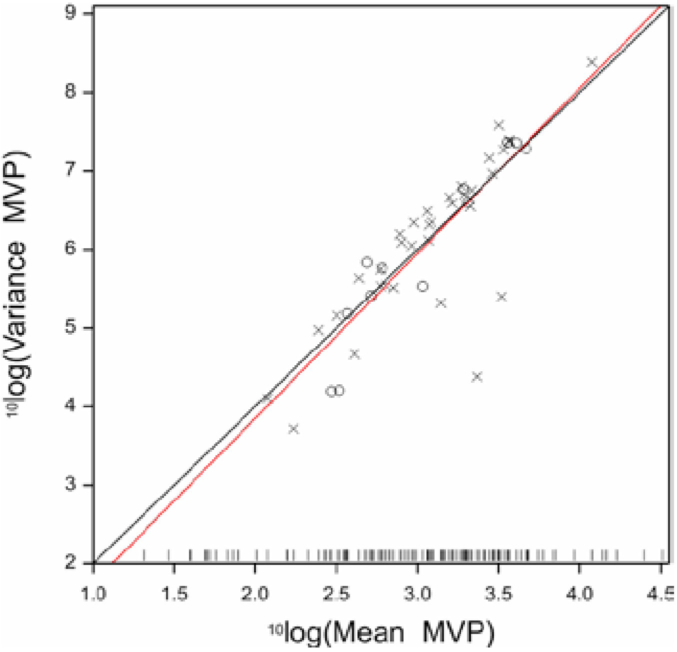

*Figure C1. The relation between log mean and log variance for mammals (x) and birds (o). The black line is Log(Variance) = 2*log(Mean) and the red line is the least squares fit. The vertical lines at the bottom of the graph represent the mean MVP estimate for all species (so also for those with only a single replicate).*

The estimates of the regression coefficients, with standard errors in parenthesis, are -0.352 (0.596) for the intercept and 2.101 (0.193) for the slope. So the intercept is not significantly different from zero, and the slope is not significantly different from 2. There is no difference between birds and mammals. We conclude that a reasonable model to describe the variance to mean relationship for MVP is Variance = Mean^2. This relationship is applied to all species including those for which only one MVP estimate is available.

Distribution of MVP

The above shows that for both mammals and birds a good description of the variance to mean relationship is given by Variance = Mean^2. We further assume that the distribution of the MVP is Lognormal with a mean μ equal to the mean of the replicates and a variance equal to μ^2. A Lognormal(λ, σ^2)) distribution has a mean $\exp(\lambda + \sigma^2/2)$ and a variance $(\exp(\sigma^2)-1)\exp(2\lambda + \sigma^2)$ (see e.g. http://en.wikipedia.org/wiki/Log-normal_distribution). Setting $\lambda = \text{Log}(\mu) - \text{Log}(2)/2$ and $\sigma^2 = \text{Log}(2)$, yields exactly mean μ and variance $\sigma^2 = \mu^2$ as desired. So we further assume that

$$\text{Log(MVP)} \sim \text{Normal}(\text{Log}(\mu) - \text{Log}(2)/2, \text{Log}(2)).$$

This distribution can also be written in terms of ^{10}Log:

$$^{10}\text{Log(MVP)} \sim \text{Normal}(^{10}\text{Log}(\mu) - {}^{10}\text{Log}(2)/2, {}^{10}\text{Log}(2)/\text{Log}(10)).$$

Note that Log(10) in these formulae is the natural logarithm.

Area requirement and Body Weight

The simplifying assumption was made that for birds, home range size is suitable for calculating individual area requirements, and for mammals, density data. A relationship between individual area requirements and body weight was obtained by regressing the ^{10}Log values of home range size (in ha) and 1/density (in km^2) on the ^{10}Log values of bodyweight (in grams) from the Damuth (1987) dataset for mammals, and the Schoener dataset updated with extra species (see Appendix A) for birds. A graphical display of these relationships is given in Figure C2.

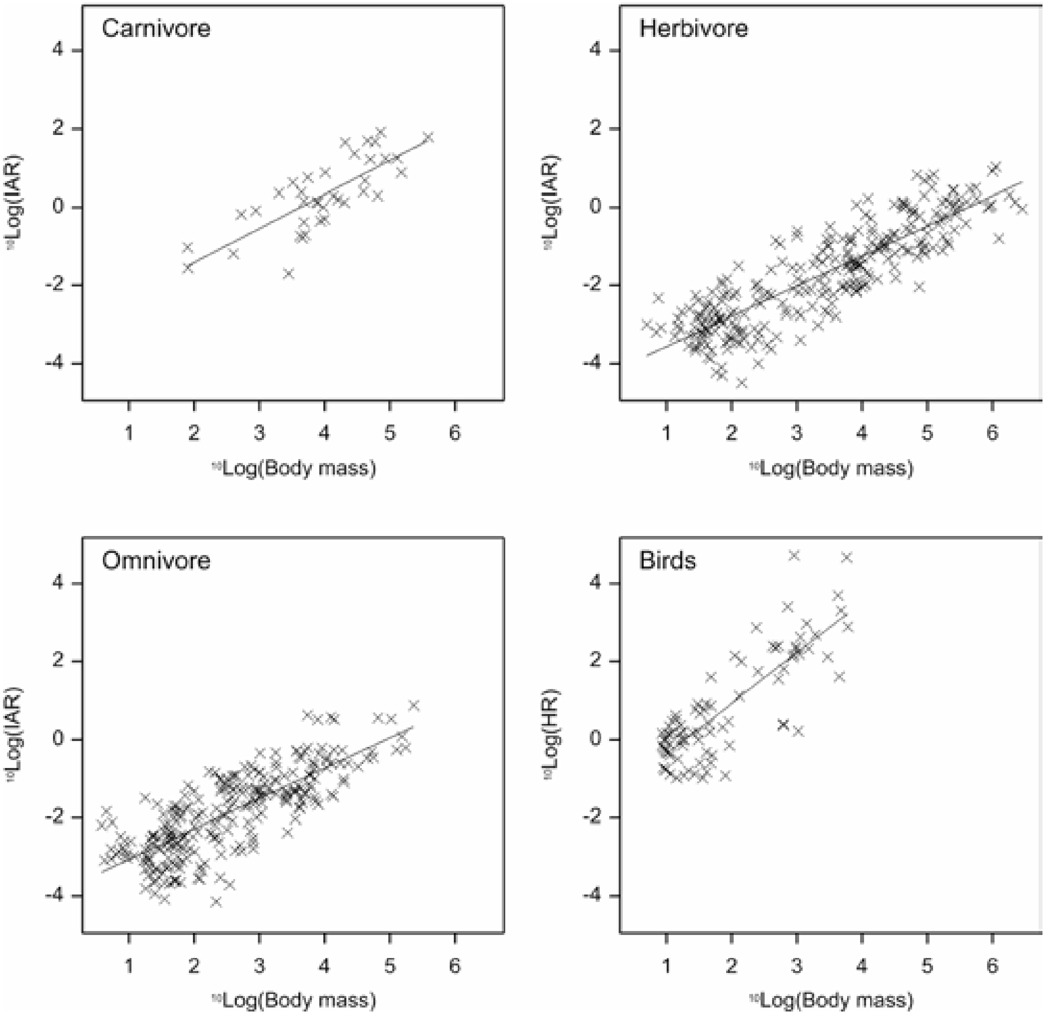

Figure C2. Regression results of ^{10}Log values of individual area requirements (mammals, in km^2) and home range (birds, in ha) on the ^{10}Log values of bodyweight (in grams) from the Damuth (1987) dataset for mammals, and the Schoener (1968) dataset updated with extra species (see appendix B) for birds.

The fit is very satisfactory for all species. Regression coefficients and their standard errors are given in Table C1 (rms stands for residual mean square which is an estimate for the residual variance).

Table C1. Results of analyses of the log-linear relationship between individual area requirements and body weight. Source of mammal data: Damuth (1987). Source of bird data: Schoener (1968) study with 77 species, supplemented with home range data from 24 species used in this study, for which area requirement values are available in literature (for the calculation, see appendix B). Standard errors of estimates are given in parenthesis and rms is the residual mean squared error.

Group	Response	Count	Slope β	Intercept α	r²	rms
Carnivore	IAR	37	0.87 (0.120)	-3.15 (0.486)	0.60	0.36
Herbivore	IAR	267	0.77 (0.028)	-4.33 (0.102)	0.74	0.41
Omnivore	IAR	256	0.78 (0.039)	-3.84 (0.106)	0.61	0.43
Birds	HR	88	1.29 (0.096)	-1.65 (0.198)	0.68	0.60

The predicted mean value of $^{10}\text{Log}(\text{AREA})$, at a specific bodyweight BWT, is then given by

$$^{10}\text{Log}(\text{response}) = \alpha + \beta\ ^{10}\text{Log}(\text{BWT})$$

where response is HR for birds and IAR for mammals. The variance, denoted by $\sigma^2(\text{BWT})$, of this predicted mean value is a quadratic function of $^{10}\text{Log}(\text{BWT})$. The distribution of the predicted mean is normal:

$$^{10}\text{Log}(\text{response}) \sim \text{Normal}(\alpha + \beta\ ^{10}\text{Log}(\text{BWT}), \sigma^2(\text{BWT}))$$

Minimum Area Requirement

Minimum Area Requirement for birds is given by:

$\text{MAR}_{\text{birds}} = \text{MVP} \times \text{HR} / 200$ which can be written as

$$^{10}\text{Log}(\text{MAR}_{\text{birds}}) = {}^{10}\text{Log}(\text{MVP}) + {}^{10}\text{Log}(\text{HR}) - {}^{10}\text{Log}(200)$$

Assuming that MVP and HR are independent random variables and using the fact that the sum of two independent normal random variables is also normally distributed, we find

$$^{10}\text{Log}(\text{MAR}_{\text{birds}}) \sim \text{Normal}(\mu_{\text{MAR}}, \sigma^2_{\text{MAR}})$$

where

$$\mu_{\text{MAR}} = {}^{10}\text{Log}(\mu_{\text{MVP}}) - {}^{10}\text{Log}(2)/2 + \alpha + \beta\ ^{10}\text{Log}(\text{BWT}) - {}^{10}\text{Log}(200)$$

$$\sigma^2_{\text{MAR}} = {}^{10}\text{Log}(2)/\text{Log}(10) + \sigma^2(\text{BWT})$$

Similarly, for mammals, Minimum Area Requirement is given by

$$\text{MAR}_{\text{mammal}} = \text{MVP} \times \text{IAR}$$

and

$$^{10}\text{Log}(\text{MAR}_{\text{mammal}}) \sim \text{Normal}(\mu_{\text{MAR}} + {}^{10}\text{Log}(200), \sigma^2_{\text{MAR}})$$

Note that the parameters α and β, and the variance $\sigma^2(\text{BWT})$, are specific for each group. A 95% interval is calculated in the usual way, e.g. for birds as
$\mu_{\text{MAR}} \pm 1.96\ \sigma_{\text{MAR}}$.

The fitted line in Figure 2B

The trendline $\alpha + \beta x$ fitted between $x = 1$ and $x = 4$ has an estimate -15.45 (1.04) for α and 28.61 (0.39) for β.

Colofon

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