



Review

Toward better application of minimum area requirements in conservation planning



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ABSTRACT

The Minimum Area Requirements (MAR) of species is a concept that explicitly addresses area and therefore can be highly relevant for conservation planning and policy. This study compiled a comprehensive database of MAR estimates from the literature, covering 216 terrestrial animal species from 80 studies. We obtained estimates from (a) Population Viability Analyses (PVAs) which explored a range of area-related scenarios, (b) PVAs that provided a fixed value – either MAR or the minimum viable population size (MVP) alongside other area-relevant information, and (c) empirical studies of occupancy patterns in islands or isolated habitat patches across area. We assessed the explanatory power of life-history traits (body mass, feeding guild, generation length and offspring size), environmental variables (average precipitation and temperature), research approach and phylogenetic group on MAR estimates. PVAs exploring area showed strong correlation between MAR and body mass. One to two additional variables further improved the predictive power. PVA reporting fixed MAR, and occupancy-based studies, were better explained by the combination of feeding guild, climatic variables and additional life history traits. Phylogeny had a consistent but usually small contribution to the predictive power of models. Our work demonstrates that estimating the MAR across species and taxa is achievable but requires cautious interpretation. We further suggest that occupancy patterns are likely sensitive to transient dynamics and are therefore risky to use for estimating MAR. PVA-based evaluations enable considering time horizon and extinction probability, two aspects that are critical for future implementation of the MAR concept into policy and management.

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1. Introduction

Space has a pivotal role in most, if not all ecological and evolutionary processes (Tilman and Kareiva, 1997). Accordingly, the selection, design and management of protected areas involve primarily the question how much area is necessary for long-term maintenance of biodiversity. A potentially important concept in this context is the Minimum Area Requirements of species (MAR), defining the amount of space (suitable habitat) that is required for the long-term persistence of a population.

Obviously, the presence of a species within a site does not guarantee its survival. First, populations occurring within remnants of suitable habitats may be declining, threatened or under an “extinction debt” from past environmental changes (Tilman et al., 1994). Second, some species may require larger area than others in order to buffer against environmental, demographic or genetic stochasticity. Therefore, a major challenge for reserve design is to ensure that sufficient protected areas contribute to the viability of as many species as possible, in consideration of both their habitat association and area requirements. Here, the MAR could be of direct relevance because of its intuitive and explicit focus on area. However, in comparison with MVP, studies dealing with MAR or providing it seem to be surprisingly limited. For instance, a search through Google Scholar (20.9.2013) for the terms “Minimum Area Requirement” + “conservation” versus “Minimum Viable Population” + “conservation” yielded 303 versus 4819 hits, respectively. Similarly, scanning 45 Species Action Plans (SAPs) covering 639 species for a set of keywords relating to PVA, MVP and MAR (see Methods), we found seven SAPs which reported the MVP, four that mentioned Minimum Area (or habitat) Requirements, but none that reported the MAR.

1.1. Factors potentially affecting the MAR

Predicting the MAR would require at least to identify important factors or traits that can explain the variation in area requirements across species and taxa. Empirical and modelling studies indicate a variety of factors that could affect the MAR, directly or indirectly. First, MAR should correlate with body mass, primarily because of energetic expenditure (Shaffer, 1981). This was demonstrated empirically by Allen et al. (1992) for mammals in mountainous regions in south-western USA, Beier et al. (2002) for birds in forest fragments in West Africa, Biedermann (2003) for reptiles, birds, mammals, and insects, and Baguette and Stevens (2013) for European butterflies.

Feeding guild or trophic levels should affect the MAR as well, since the availability and energetic contents of food affect the area required by individuals. Hechinger et al. (2011) have shown that inclusion of trophic level is imperative when searching for scaling

rules for energy use, and further evidence supports the importance of feeding guild in describing spatial attributes such as home range size and dispersal distance (Harestad and Bunnell, 1979; Kelt and Van Vuren, 2001; Lindstedt et al., 1986; Mace et al., 1982; Ottaviani et al., 2006; Sutherland et al., 2000). Yet some studies found inconsistent patterns with respect to trophic levels (Dardanelli et al., 2006; Ottaviani et al., 2006) – possibly because food availability (and other essential ecological resources), which relates to trophic level (albeit loosely), affects space use as well.

Species' demography is another factor which likely affects area requirements, where “K”, or slow species along the slow-fast continuum (e.g. Burton et al., 2010), might require larger areas than “r”, or fast species. This relates to their larger body size (Biedermann et al., 1999; Henle et al., 2004a) as well as longer life which may entail greater resource limitation. Note, however, that demographic stochasticity and population responses to environmental stochasticity play important roles in determining population viability, and hence area requirements, with higher variability leading to larger area requirements (Shaffer, 1987; Soulé, 1987; Thomas, 1990).

Species' demography is affected also by dispersal traits and the response of species to landscape characteristics (Burton et al., 2010). Biedermann (2003) suggested that predictions of area requirements could be improved by considering variables such as patch isolation and species traits, and Swihart et al. (2003) found that body size was an inferior predictor of tolerance of fragmentation compared to niche breadth and proximity to range boundary. Baguette and Stevens (2013) have shown that four life history traits (thermal requirements, mating strategy, capital- versus income-breeding strategy and affiliation with ants), alongside wing size, substantially improve the capacity to explain variability in the area requirements of European butterflies. Most of these traits strongly relate to energy and space-use. These examples demonstrate the challenges in deriving an area estimate that is truly independent of the effects of patch networks (e.g., metapopulations), including landscape connectivity.

As the traits of species relate to their taxonomic affiliation or phylogeny, its consideration could further enhance the capacity to explain variability in MAR estimates. Especially if considering different taxa, one must account for very different means of thermal regulation (ectotherms versus endotherms) or locomotion, that could result in large differences in MAR versus body mass. Evidence for cross-taxa differences was found by Silva et al. (1997), showing that birds have a much lower density per body mass compared to mammals and thus likely their area requirements should be larger. Even within a taxonomic group (across butterfly species), inclusion of phylogeny as a variable had slightly contributed to improving MAR predictions (Baguette and Stevens, 2013).

Finally, climate and weather, including environmental variability, are critical components affecting the MAR. The climatic context predefines productivity and food availability, but a clear directional effect on the MAR is difficult to postulate because population densities can be low even if climatic conditions are favourable. More importantly, environmental stochasticity affects the minimum viable population size, with higher variability requiring larger populations in order to sustain a viable population (Shaffer, 1987; Verboom et al., 2001). Consequently, Verboom et al. (2010) suggested that MARs may increase in response to enhanced climatic variability associated with climate change (IPCC, 2007).

In summary, the multitude of factors that can potentially affect the area requirements of species, the interrelation between them and their combined impacts, render it challenging to form clear expectations regarding the predicted MAR value for a species or taxon (e.g. Fahrig, 2007). However, analyses across species and taxa, and inclusion of relevant traits of species and their environment in analyses, can substantially improve our capacity to understand, generalize, and potentially predict the MAR. Therefore, one of the main purposes of this contribution is to identify important factors that can be useful to predicting MAR across species, using an exhaustive database of published estimates. To do this, one must collect and standardize MAR estimates across studies, with careful consideration of the study approach, units used, and threshold set for defining viability (Table 1).

1.2. How to estimate MAR?

One could obtain an estimate of the MAR in various ways. One central approach involves using simulation models to identify thresholds under which population viability diminishes, i.e., Population Viability Analyses (PVA) (Beissinger and McCullough, 2002). PVAs may yield estimates of the MAR either by exploring a range of hypothetical areas, or by assessing minimum viable population size (MVP) and providing it alongside other area-relevant measures, such as population density. Another approach is based on observed occupancy patterns across a range of habitat area (Allen et al., 1992; Baguette and Stevens, 2013; Diamond, 1978; Dunn and Loehle, 1988; Lomolino, 2000). Estimates can be based on historical data (extinction patterns) or current occurrence, on real islands or isolated patches of suitable habitat (e.g. mountain tops). This paper presents a database that brings together MAR estimates originating from these different approaches. We then explore whether MAR estimates can be explained by a combination of

physiological, demographic, ecological and climatic variables, as well as taxonomy or phylogeny.

2. Methods

2.1. Dataset and literature search

This study focuses on terrestrial animals, which share sufficiently comparable body plans and ecological constraints. However, the approach we used could be transferable, *mutatis mutandis*, to plants or aquatic organisms. Data were obtained from published articles, book chapters and, where possible, monographs, PhD theses and conference proceedings available through university library databases. Primary literature was identified through a list of PVA studies compiled by Henle et al. (2004b) for an analysis of density-dependent effects on population dynamics. The list now comprises of 450 sources and 225 species published since 1976. A second database synthesized data from 78 published PVA studies of terrestrial animals, summarizing circa 260 parameters including input and output parameters (Pe'er et al., 2013). We further used the online appendix from a review of PVAs by Traill et al. (2007), containing MVP estimates for 287 studies. From this database, we extracted cases where additional information was provided on MAR, population density or study area. IUCN Red lists (IUCN, 2006) provided further cases where MVP and population density were reported. We complemented our database by a search through ISI Web of Science and Google Scholar, using the search terms “minimum area requirements”, “minimum critical habitat/area”, “minimum suitable habitat”, “minimum required habitat”, “minimum habitat requirements”, or “MAR”. To confine the search results we used the terms “conservation ecology” or “ecological model*”. We additionally searched for single words or phrases that contain combinations of the terms MAR, area, MVP, and PVA (including full words and acronyms). Somewhat similar keywords were also used for scanning within 45 Species Action Plans (SAPs) covering 639 species, as well as 5 SAPs covering entire taxa (>11,000 species in total). Whenever identifying MAR estimates, we sorted them based on study approach dividing into (a) PVAs exploring a range of areas (hereafter, explorative PVAs) (Appendix A Table A1), (b) PVAs providing an estimate of the MAR or an estimate of MVP alongside other area-relevant information yet without exploring area (hereafter, fixed-MAR estimates) (Appendix A Table A2), and (c) occupancy-based estimates of MAR (Appendix A Table A3).

Table 1
Number of cases and studies providing estimates of the MAR of species, divided according to approach and taxonomic groups (I = Insects, R = Reptiles, B = Birds, M = Mammals, Σ = Total number of species). Studies providing the MAR as is and studies providing MVP alongside other area-related measures were clustered in all analyses as both reported a fixed number without exploring area.

Approach	How MAR was obtained or calculated	Cases ^a	# MAR estimates				
			I	R	B	M	Σ
PVA	PVA explored areas (threshold set by us)	25	8	1	9	13	31
Fixed-MAR: MAR provided by authors	Study area reported	12	0	1	3	8	12
	MAR reported as is by authors	22	3	0	6	13	22
	MAR given by authors/questionnaire-based	1	0	0	0	1	1
	MAR given by authors based on study area	1	1	0	0	0	1
Fixed-MAR: MVP-based	MVP/density	10	0	0	3	7	10
	MVP/density/study area	4	0	0	1	3	4
	MVP/study area	1	0	0	0	1	1
	MVP \times Home-range	1	0	0	1	0	1
Occupancy-based	Based on 30% occupancy threshold	1	0	0	31	0	31
	Based on 50% occupancy threshold	3	0	0	85	0	85
	Based on 80% occupancy threshold	3	0	0	12	0	12
	Based on 90% occupancy threshold	1	5	0	0	0	5
Total		85	17	2	141	46	216

^a The number of cases is larger than the number of studies (80) as some studies took more than one approach to report the MAR or related values.

2.2. Extracting estimates of the MAR from PVAs that explored area

To obtain data from PVA studies that explored a range of areas, we defined the MAR as the threshold point where the probability of extinction exceeds 0.05 within a time horizon of 100 years. In the case that the probability of extinction was provided for a different time horizon, we applied the function $P_0(t) = 1 - e^{-t/T_m}$ where $P_0(t)$ is the probability to reach a population size of zero within a time horizon t , and T_m is the intrinsic mean time to extinction (Grimm and Wissel, 2004). We set T_m to 1950 years, as this value would yield $P_0(t) < 0.05$ for a time horizon $t = 100$ years. We note that applying this equation assumes that simulations have reached an established phase where population viability is no longer affected by the initial conditions (Grimm and Wissel, 2004). We excluded studies where population size at initial conditions was clearly smaller than half of carrying capacity of patches (V. Grimm, personal comm.).

Once defining the necessary threshold for a given study, we explored the representation of extinction probabilities versus area, using tables to reconstruct the functional relationship or visually exploring graphs, if provided, to extract the MAR at the selected threshold. We conducted a sensitivity analysis with alternative time horizons (10, 50 or 100 years), as well as a threshold extinction probability of 1%. This analysis indicated very marginal impact on the overall outcomes (results not shown), and hence we regard the selection of viability threshold as non-critical in this case. For further discussion on the choice of viability measures and time horizon, see Pe'er et al. (2013) and Franz (2011).

2.3. Database construction and data standardization

For each study, we registered the source, species name, study site location, how the MAR was derived, the threshold value used to define viability (i.e., probability of extinction, or occupancy level for empirical studies), and, for PVA studies, time horizon if reported, and whether the model was applied for a single population or a metapopulation. When authors reported more than one estimate, we registered the minimum and maximum estimates (= scenarios) provided, as well as the mean or baseline scenario if indicated by the authors (i.e., most plausible scenario). Where possible, we extracted information also of home range size, including the percent overlap in home-ranges. Finally, we registered the units used by authors to report the MAR, and standardized them to derive the MAR in terms of area in hectares. Where necessary, we searched for complementary publications that could enable this standardization: e.g., some studies reported the MAR in terms of number of territories or home ranges, but their area was available elsewhere.

2.4. Testing the factors explaining the MAR

To gain first insights on the contents of our database we plotted the frequency distribution of MAR estimates, and then the singular values against body mass (both \log_{10} -transformed) for each of the three methods of deriving the MAR. We then tested the effect of eight explanatory variables on the MAR: (1) the method to estimate the MAR, (2) body mass, (3) number of offspring per reproduction event, (4) generation length, (5) feeding guild (frugivore, carnivore, insectivore, omnivore or herbivore/granivore), (6) mean annual temperature and (7) mean annual precipitation at the study site, and (8) taxonomic group. MAR and all quantitative explanatory variables were log-transformed. To derive information on these predictors, we used available trait databases of the SCALES project (<http://www.scales-project.net>), Prugh et al. (2008), or published papers on the focal species. Climate information was extracted from the WorldClim website (<http://www.worldclim.org>). For a full list of data sources see Appendix B.

To investigate the relative importance of each variable for MAR, we fitted a series of generalized linear mixed-effects models (GLMM) using R (R Development Core Team, 2004), applying the lmer function (lme4 library; Bates et al., 2013). We used the random effects error structure of GLMM to correct for non-independence of species due to potential taxonomic relatedness. We also repeated the analyses using a series of generalized linear models (GLM) with the same predictors but considering species as independent units. Differences between GLM and GLMM outcomes could then serve as a measure of the effect of taxonomic affiliation. We explored collinearity among predictor variables using tolerance levels (Quinn and Keough, 2002), and Goodman and Kruskal's gamma to test for categorical variables against other variables. Based on these, we removed variables that were highly correlated to others (e.g. body length). Tolerance levels for the remaining variables were sufficiently high (i.e. greater than 0.1, following Quinn and Keough, 2002) and Goodman and Kruskal's gamma coefficients low enough (<0.4) to allow inclusion of those variables included here (Appendix C Table C1). Prior to the analysis we also tested whether any of the predictors should be modelled using linear or polynomial terms, by regressing the MAR against each of the predictors separately, in both forms. As none of the quadratic relationships were significant (Appendix C Table C2), we used only linear terms. We started with a full model with all predictors, including interactions between (a) body mass and each one of the predictors, (b) temperature and precipitation, and (c) generation length and the number of offspring. We then removed variables that were clearly insignificant. To select among the multiple models, we used Akaike's information criterion (AICc) as a measure of overall model fit (Burnham and Anderson, 2002). The top ranked models (within 4 points of AICc) were then averaged as implemented in the MuMIn R-package (Barton, 2012). When performing the analyses for all taxa and all three approaches together, we excluded the climatic variables. This is because most empirical studies addressed multiple species, thus biasing the number of cases with similar climate. In a second analysis, we excluded the empirical studies and assessed the impact of all explanatory variables on MARs derived from the two PVA-based approaches only. We also repeated the analysis for each of the three approaches separately, as well as for mammals and birds separately (the only taxa for which sufficient data were available for a separate analysis). We compared GLMM models with GLMs in terms of the parameters identified as important for explaining the MAR, as well as according to their overall performance in terms of the percentage of the total deviance explained. For the best fit GLM and GLMM models ($\Delta\text{AICc} = 0$) we used the calc.relimp procedure implemented in R-package 'relaimpo' (Groemping, 2013) to decompose the variance of the final model among the different predictors and interactions. Finally, we performed a phylogenetic generalized least-squares regression (PGLS; Martins and Hansen, 1997) to test whether any phylogenetic effects remain which were not captured by the GLM. This analysis focused on European birds using phylogenetic trees from Thuiller et al. (2011), and mammals, using the trees from Fritz et al. (2009). We computed branch lengths based on Grafen (1989). We conducted the PGLS with the R packages 'ape' (version 2.15–3; Paradis et al., 2004) and 'caper' (version 0.4; Orme et al., 2011).

3. Results

3.1. MAR availability in the literature

After sourcing and filtering 870 relevant studies published between 1976 and 2011, addressing 1163 species, we found 80 studies that met the selection criteria, providing MAR estimates for 216 species. Some studies reported several species, and estimates for some species were available from more than one

study (Table 1). Out of these, 25 PVA studies performed a systematic exploration of area or related units, providing estimates for 31 species. The units of the MAR as provided by these studies varied greatly and included area, number of territories, carrying capacity or number of individuals, number of patches, or other measures, not all of which could be translated into area (Table 2). We found 50 PVA papers (52 cases covering 47 species) that provided either the MAR as it is (36 cases) or MVP alongside density (16 cases) (Table 1). We found 11 empirical studies providing occupancy-based estimates of the MAR. These covered 133 species, 128 of which were birds (Table 1). Studies that obtained MAR estimates through a semi-quantitative evaluation based on expert opinion (Bink, 1992, 142 butterfly species), obtained the MAR by other means or did not clearly report the means to obtain it (74 cases), were excluded from analyses in this study. For a full list of species, methods and sources, including extracted values, see Appendix A.

Overall, MAR estimates were available primarily for birds and mammals, with only some values for insects and reptiles, and not a single study found for amphibians or other taxa (Table 1). MAR values themselves ranged from 0.1 (butterfly, froghopper) to 3,500,000 ha (Scandinavian wolverine), and the frequency distribution suggested a strong tendency to address animals with large area requirements (Fig. 1).

MAR estimates originating from explorative-PVAs have shown a significant log–log linear relationship between MAR and body mass for all scenarios, namely the average (or baseline) ($R^2 = 0.598$, $df = 12$, $p < 0.01$), minimum ($R^2 = 0.571$, $df = 19$, $p < 0.01$) and maximum

scenarios when provided by authors ($R^2 = 0.624$, $df = 19$, $p < 0.01$) (Fig. 2a). The same qualitative results were obtained for fixed-MAR estimates (Fig. 2b), but no relation was found between MAR and body mass for estimates originating from occupancy-based studies (Fig. 2c). Because of the high correlation in MAR values between the three scenarios (R^2 values > 0.95), results hereafter are presented only for the baseline scenario.

3.2. Traits and environmental factors affecting the MAR

Analysis of the predictive parameters of the MAR for all methods and taxa found two candidate GLMM models with

Table 2
Units used for reporting MAR by PVA studies exploring area. The units listed herein include only those that were defined by the authors as being a measure of the MAR.

MAR measure	Number of cases
Area	9
Number of territories	5
Number of flower-heads ^a	4
Number of patches	4
Carrying capacity (# individuals)	4
Population size	1
Habitat width	1
Number of home ranges	1
Number of pairs	1
Number of trees ^a	1
Patch size (ha)	1

^a As a habitat.

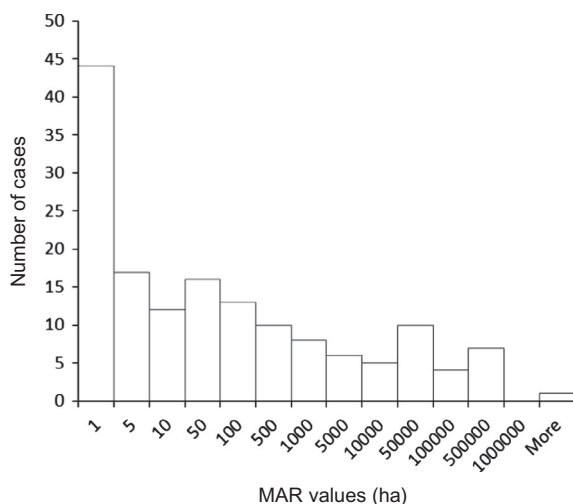


Fig. 1. Frequency of reported MAR estimates.

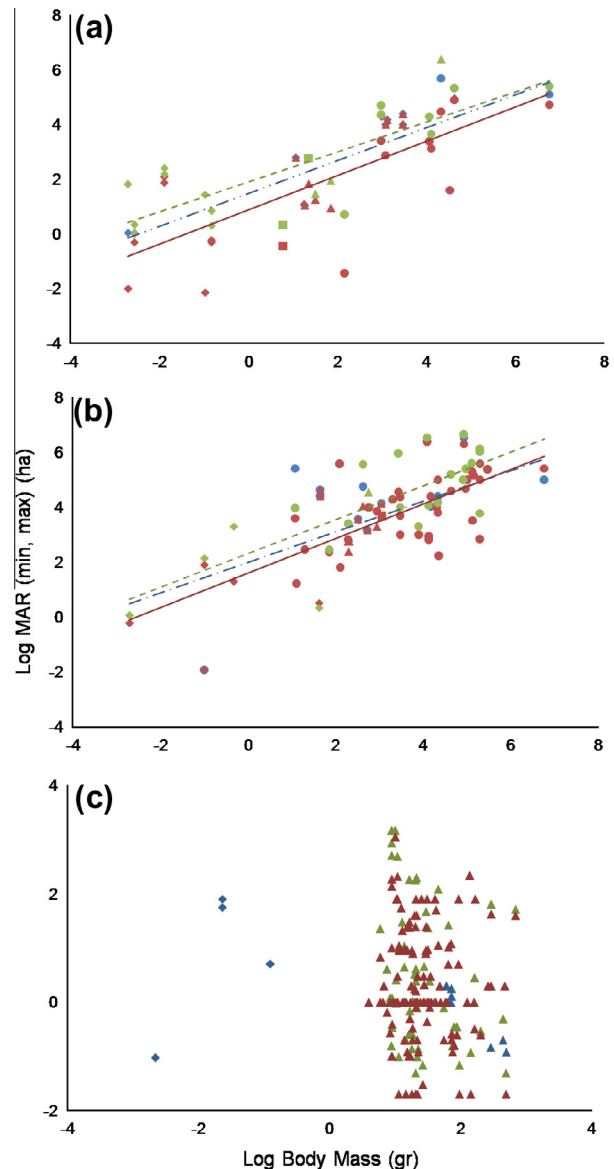


Fig. 2. Relationship between body mass and the minimum area requirements based on the different ways MAR were derived, (a) based on PVA papers that explored a range of areas (based on a threshold value set by us); (b) based on PVA papers where authors provided MAR or MVP alongside area-relevant information (density or study area); (c) based on empirical studies of % occupancy versus area, and separated into taxa. Blue = average, Red = minimum, Green = maximum values for MAR. Circles = mammals; triangles = birds; diamonds = insects; squares = reptiles. Where minimum or maximum values were not provided by authors, we listed the MAR as the mean or baseline scenario. Regression lines are provided only for significant relationships. Dashed green line = average, solid red line = minimum, dashed-dotted blue line = maximum.

$\Delta AICc < 4$, containing “method” as a prime explanatory variable (occupancy-based estimates yielding lower estimates), followed by body mass, feeding guild, and the number of offspring. Generation length occurred in one of the two models, due to an increase in MAR with generation length (Table 3a). The use of GLMs increased the explained deviance from 65% to 69%, with two candidate models containing the same explaining variables as the GLMMs, alongside “taxon”.

When excluding the occupancy-based studies and focusing on the two PVA-based approaches (Table 3b), body mass became the dominant factor, explaining 52.9% of the total deviance and occurring in all plausible GLMMs and GLMs. Other explanatory factors included in the plausible GLMMs were temperature and generation length; Method occurred only in one model. The use of GLMs increased again the overall performance (from 53.5% to 57.76% of the total deviance explained), producing 13 candidate models. Temperature and/or rain, as well as interactions between the two, occurred in 10 of 13 models and indicated an increase in MAR with temperature or precipitation, rather than a decrease as one may anticipate; 7 GLMs included Method, 3 included generation length and 3 included feeding guild. Predictive GLMMs for explorative-PVAs alone were dominated again by body mass as the best predictor, and accompanied by rain and/or temperature (7 of 9 cases) and generation length (Table 3c). GLMs yielded similar results, again with a slightly higher predictive power.

For PVAs that provided a fixed estimate, feeding guild had the highest explanatory power (MAR for carnivores > insectivores > herbivores), but it explained only 19.8% of 53.9% of the total deviance (Table 3d). Generation length and temperature occurred in all plausible GLMMs and GLMs, the number of offspring was included in most (indicating slightly smaller MAR for species with higher number of offspring), and body mass occurred in two of the three GLMs. Interestingly, in these two models feeding guild was not included.

For occupancy-based studies (Table 3e), the candidate models were generally more complex and included a larger number of parameters as well as interactions between them. The best predictor was feeding guild. Generation length and the number of offspring were included in all selected GLMMs, whilst body mass was included in 3 out of 4. GLMs did not explain a higher proportion of the deviance, but introduced an impact of “taxon” – thereby explaining the outcomes obtained for all methods together (c.f. Table 3a).

When focusing on mammals alone (based on the two PVA-based approaches; Table 3f), a GLM identified body mass or body mass with generation length as the best models, yet only 20% of the overall deviance was explained. A PGLS performed slightly better, but interestingly indicated body mass and temperature and/or rain to serve as the most important parameters. Two of 5 models also included method as an explaining variable. Similar analysis for European birds (Table 3g) found a single plausible GLMM explaining 56% of the deviance, including feeding guild (best predictor) alongside body mass and method. The use of PGLS in this case increased performance to 73.5% and strengthened the explaining power of feeding guild. The method was included in all 3 selected PGLSs. Body mass, or the number of offspring, were included in 1 of 3 models each.

Finally, analysis for European birds using occupancy-based approach (Table 3h) found feeding guild to be the dominant explanatory variable, alone or alongside either the number of offspring or body mass. The same three candidate models were found through GLM or PGLS, yet the power of PGLS was substantially higher (49.6% versus 38.5% of the total deviance explained).

Drawing MAR estimates against body mass, with different clustering options of the data, show that empirical studies strongly deviate from the two other approaches (Fig. 3a). Taxonomic groups

are visually aligned along one axis of MAR versus body-mass (Fig. 3b1), especially when removing the empirical studies (Fig. 3b2) but yielding differing slopes if focusing on each taxonomic group separately (especially insects). The signal of feeding guild can also be clearly seen, where carnivores > insectivores > herbivores (Fig. 3c1 and c2).

To summarize, statistical models explained a varying range (20–73%) of the deviance in MAR estimates between species or taxa, with best predictive power when using PVA-based approaches (especially for birds alone), and worst performance for mammals or when using occupancy-based MARs. MARs from explorative-PVAs were best explained by body mass alone or alongside one or two parameters, one relating to life cycle strategies (generation length) and the other relating to environment (rain or temperature). Fixed-PVA approaches indicated a clear relation with body mass as well, but found feeding guild to be the best predictor of the MAR. Yet it had less power as a single explanatory variable, requiring a larger number of parameters to explain the MAR. Occupancy-based estimates required the most complex models, and were best explained by the combination of feeding guild, both life-history traits, and body mass (alone or in its interaction with other factors). Finally, in almost all cases, model performance slightly improved from GLMM to GLM and further to PGLS. This indicated a weak but consistent phylogenetic effect, but it did not alter the overall pattern in terms of the variables explaining the MAR. For birds, however, we found a somewhat stronger within-taxon phylogenetic effect.

4. Discussion

4.1. MAR estimates are available for many species

In an extensive literature search, this review identified available quantitative MAR estimates in 80 studies, covering 216 species. Most studies focused on birds and mammals, indicating that the concept is applied for merely a handful of taxonomic groups. However, the concept may clearly be equally applicable to other groups, as demonstrated recently by [Baguette and Stevens \(2013\)](#) for butterflies and supported by a bulk of theoretical and empirical studies indicating that area correlates with population size, and the latter correlates with population viability ([Soulé, 1987](#)). Many studies had to be excluded due to partial reporting, e.g., not reporting the method for estimating the MAR, reporting MVP but not density, or providing the number of species occurring across patch (or island) sizes but without further information at the species level. With 74 cases that had to be excluded from analyses ([Appendix A Table A4](#)), and many cases within SAPs where authors reported MVP or density but the MAR could not be extracted, we are certain that the number of available MAR estimates could easily extend if attention is given by authors to reporting it.

Results using PVAs that explored area to extract the MAR indicated body mass as one of the key predictors of the MAR of species. One or two life history traits, or alternatively environmental factors such as the mean annual temperature or the average precipitation at the study region, further improved the capacity to predict the MAR, but hinted that the impact of the explaining variables is not necessarily intuitive: e.g., MAR increased with both temperature and precipitation. Fixed MAR estimates yielded quite consistent results (Fig. 3a) but could be explained either by body mass (Fig. 2b) or feeding guild combined with other factors (Table 3d). This may relate to a potential replaceability between feeding guild and body mass, likely due to food density (and not the energetic contents of food, which would entail an opposite effect of feeding guild). Yet it also indicates a risk in using a fixed value, especially MVP, which in itself is affected by various factors

Table 3

Ranking of alternative generalized linear mixed models and generalized linear models (GLMM on left side, GLM on right side), or between GLMs and phylogenetic generalized least-squares regression (PGLS), using Akaike's Information Criterion corrected for small sample sizes (AICc). MAR estimates were tested against body mass (MASS), generation length (GNL), the number of offspring (OFF), feeding guild (FEED), taxon (TAXON), temperature (T°) and precipitation (RAIN) at the study site, and the method to derive the MAR (METH). Taxonomic class served as the random effect in GLMMs. Results present (a) all approaches and taxa together; (b) PVA-explorative and fixed-MAR approaches; (c) PVA-explorative approach alone; (d) fixed-MAR approach alone; (e) occupancy-based studies alone; (f) mammals only and (g) European birds only, based on the two PVA-based approaches; and (h) European birds only, based on occupancy-based studies. We only list candidate models with $\Delta AICc < 2$. Models are summarized by the total deviance explained ($\% \sum dev$) for all selected models. We further list the factor explaining the largest proportion of total deviance, alongside the $\% dev$ explained by that factor, for the best model ($\Delta AICc = 0$).

Candidate models	$\Delta AICc$	$\% \sum dev$ (best)	Candidate models	$\Delta AICc$	$\% \sum dev$ (best)
<i>(a) All approaches and taxa together</i>					
GLMM			GLM		
MASS + OFF + FEED + METH	0.00	65.32		0.00	69.38
MASS + GNL + OFF + FEED + METH	1.43	(METH 21.3)	MASS + GNL + OFF + FEED + METH + TAXON	1.83	(METH 24.6)
<i>(b) Two PVA-based approaches (together)</i>					
GLMM			GLM		
MASS + T°	0.00	53.49	MASS + T°	0.00	57.76
MASS	0.50	(MASS 52.9)	MASS + METH + T°	0.18	(MASS 56.6)
MASS + METH + T°	0.89		MASS + METH + T° + RAIN + T° * RAIN	0.27	
MASS + GNL + T°	1.66		MASS	0.27	
MASS + GNL	1.88		MASS + METH	1.21	
			MASS + FEED + METH + T° + RAIN + T° * RAIN	1.49	
			MASS + T° + RAIN + T° * RAIN	1.57	
			MASS + OFF + FEED + METH + T°	1.58	
			MASS + FEED + METH + T°	1.67	
			MASS + OFF + T°	1.89	
			MASS + GNL + METH + T°	1.93	
			MASS + GNL	1.95	
			MASS + GNL + T°	1.95	
<i>(c) PVA-explorative approach</i>					
GLMM			GLM		
MASS + GNL	0.00	51.27	MASS + GNL	0.00	53.68
MASS + GNL + T°	0.04	(MASS 41.22)	MASS	0.24	(MASS 44.97)
MASS + GNL + RAIN	0.71		MASS + RAIN	0.71	
MASS + T°	0.75		MASS + T°	1.21	
MASS + GNL + RAIN + T°	1.00		MASS + GNL + MASS * GNL	1.44	
MASS + RAIN + T°	1.33		MASS + RAIN	1.71	
MASS + RAIN	1.40		MASS + GNL + RAIN	1.73	
MASS	1.53		MASS + GNL + T°	1.77	
MASS + T°	1.92				
<i>(d) PVA-fixed approach</i>					
GLMM			GLM		
GNL + OFF + FEED + T°	0.00	53.87	GNL + OFF + FEED + T°	0.00	56.18
GNL + OFF + T° + GNL * OFF	1.45	(FEED 19.84)	MASS + GNL + OFF + T°	0.82	(FEED 26.05)
GNL + OFF + FEED + T° + GNL * OFF	1.97		MASS + GNL + T°	1.93	
<i>(e) Occupancy-based approach</i>					
GLMM			GLM		
MASS + GNL + OFF + FEED + MASS * GNL + MASS * OFF + MASS * FEED + GNL * OFF	0.00	44.08	MASS + FEED + TAXON + MASS * TAXON	0.00	44.62
GNL + OFF + FEED + GNL * OFF	0.67	(FEED 22.72)	MASS + GNL + FEED + TAXON + MASS * TAXON	1.31	(FEED 20.55)
MASS + GNL + OFF + FEED + MASS * FEED + GNL * OFF	1.09				
MASS + GNL + OFF + FEED + MASS * GNL + MASS * OFF + GNL * OFF	1.17				
<i>(f) Mammals only, based on the two PVA-based approaches</i>					
GLM			PGLS		
MASS	0.00	20.3	MASS + METH + T°	0.00	22.10
MASS + GNL	0.69	(MASS 17.28)	MASS + T°	0.08	(MASS 10.15)
			MASS + METH + RAIN	1.20	
			MASS + RAIN	1.37	
			MASS + T° + RAIN	1.47	
<i>(g) European birds only, based on the two PVA-based approaches</i>					
GLM			PGLS		
MASS + FEED + METH	0.00	56.36	FEED + METH	0.00	73.5
		(FEED 43.09)	OFF + FEED + METH	0.14	(FEED 51.34)
			MASS + FEED + METH	1.04	
<i>(h) European birds only, based on occupancy-based approach</i>					
GLM			PGLS		
FEED + OFF	0.00	38.46	FEED	0.00	49.63
FEED	0.23	(FEED 32.96)	FEED + OFF	0.61	(FEED 25.02)
FEED + MASS	1.95		FEED + MASS	0.77	

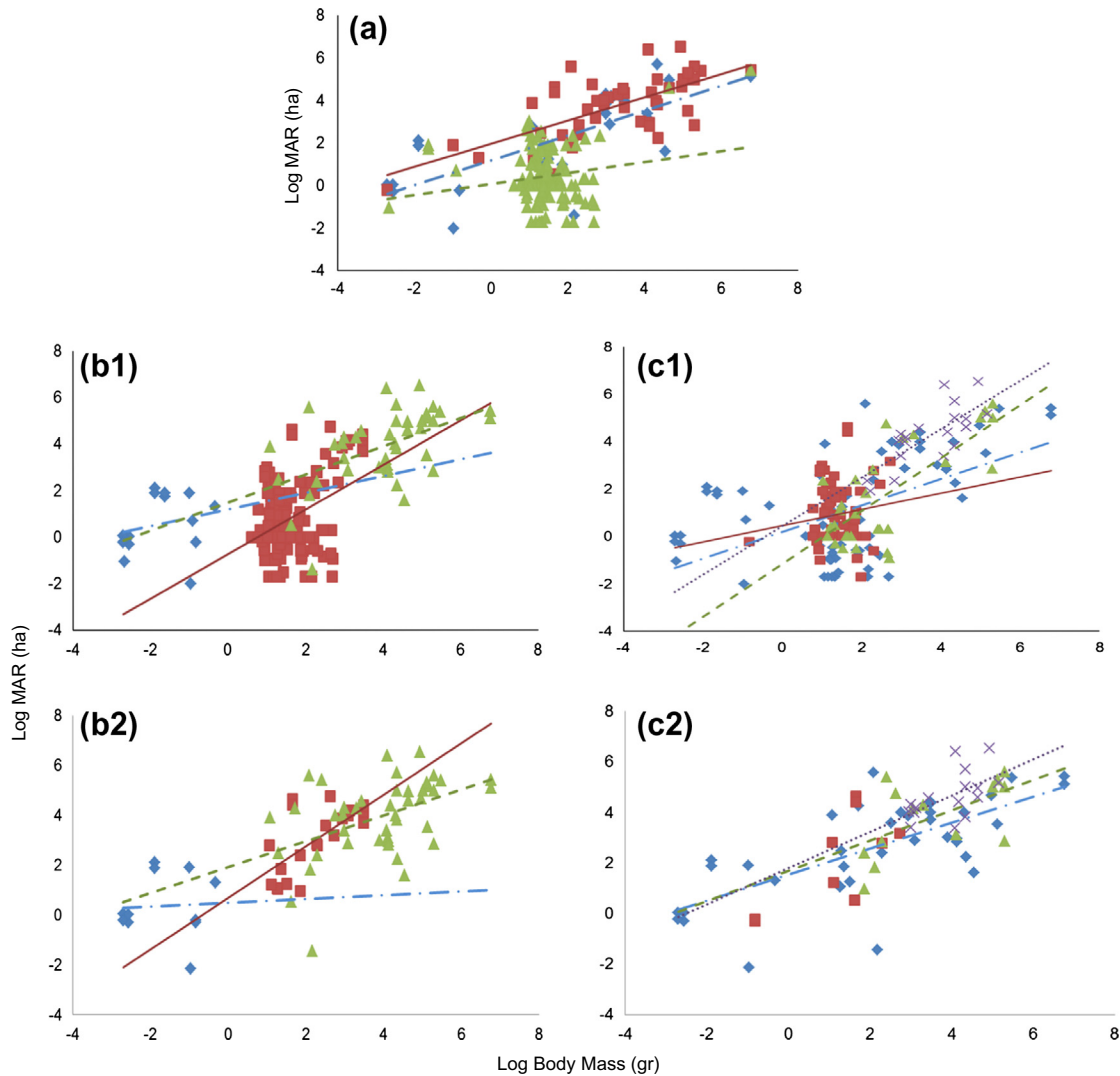


Fig. 3. MAR versus body mass, with alternative clustering of MAR estimates for visual demonstration of the impact of important explanatory variables: (a) full dataset with 3 approaches and all species, divided into different methods (blue diamonds = PVAs exploring area, red squares = MVPs, green triangles = Occupancy based studies); (b1) full dataset, divided according to taxa (blue diamonds = insects, red squares = birds, green triangles = mammals); (b2) same as b1 but without occupancy-based studies; (c1) full dataset, divided according to feeding guild (blue diamonds = herbivores/granivores/frugivores, red squares = insectivores, green triangles = omnivores, purple crosses = carnivores.); (c2) same as c1 but without the occupancy-based studies. We depict regression lines only where significant trends were found.

including density (Isaac et al., 2013). This may explain the complexity of models that were required to explain the deviance in MAR between species and taxa for estimates originating from studies reporting a fixed PVA. We should further note that 65% of PVAs that explored area reported a range of MAR estimates for alternative scenarios, yet only 44% of the papers that reported a fixed MAR or MVP provided a range of possible estimates. Potentially, such a gap in reporting could be partly resolved by generating confidence intervals *a posteriori*, considering that the minimum, average and maximum values were highly correlated.

4.2. Occupancy patterns and the relation between body mass and MAR

The complexity of models predicting the MAR from occupancy patterns, the weak or indirect relation to body mass (cf. Fig. 2c) and the deviation from MAR estimates predicted by PVA-based approaches (Fig. 3a) can be interpreted in two opposing ways. One is that occupancy may be inappropriate for estimating the area requirements of species, because occurrence in a given time is not necessarily an indicator of suitability or long-term viability.

We suggest that occupancy patterns might be useful for estimating the MAR if isolation occurs for long periods (e.g., hundreds or thousands of years) or for short-living organisms (Baguette and Stevens, 2013).

An alternative explanation could be that MAR reflects a combination of factors that only correlate with, or interact with, body mass in a more intricate way – feeding guild being one of the most relevant trait relating to energy-use and hence, potentially, replacing body mass as an explanatory variable. In other words, the complexity of interacting factors reveals a (true) relation between occupancy, detectability and density. The latter relates to body mass (Isaac et al., 2013) but includes compensatory mechanisms where small populations of low density may require the same space as large populations with high density, depending on species' demography and their sensitivity to environmental stochasticity (see Isaac et al., 2013 for further discussion). Such links are impossible to reveal through PVAs because they use density as an input. This interpretation may be supported by the fact that, for occupancy-based studies, the best statistical models included several interactions between body mass and other factors (Table 3e).

Taken together, a more careful inspection of occupancy studies, originating from different approaches, is required in order to gain better understanding of the potential realms of applicability of the approach for estimating the MAR.

4.3. PVAs: a lane to predictions?

Ecological models offer the means to yield valuable estimates of the MAR. PVAs in particular enable exploring which parameters affect viability, separating effects of connectivity from the “real” viability of isolated populations (Bender et al., 1996; Hildenbrandt et al., 1995), and incorporating time horizon and extinction probability into the estimates. PVAs further enable assessing and quantifying uncertainty. However, there are some important caveats. First, some reported MAR estimates originate from metapopulation studies. Here, authors must validate that the MAR reflects population viability irrespective of connectivity or the general dynamics of the patch network. This was rarely reported by authors. Second, since many PVAs address species or populations at risk, the data they rely on may be biased by system instability, potential extinction debt or genetic stochasticity and bottlenecks, all of which can easily bias estimates of the MAR. This requires a careful examination of such potential biases. Finally, the need to encapsulate uncertainty often results in such a broad range of estimates that the values have little applicability to planning or policy. Moreover, careful yet excessively high estimates may disqualify the use of MAR estimates in decision making if deemed unreasonable. We therefore recommend authors report a range of scenarios while delineating which factors are responsible for the differences between different estimates of the MAR. Conservative estimates can then be adopted in decision-making, whereas mean values can serve for extrapolations to other species.

An important related question that emerges from our analyses is how to identify a value that can be considered as ‘correct’, applicable, or relevant for decision making. We assert that in decision-making under uncertainty, there is probably no such value because ‘correctness’ depends on the perception of viability and the target for conservation (Brook et al., 2002; Burgman, 2001; Burgman et al., 1993; Possingham et al., 1993). To overcome this challenge, we recommend translating MAR estimates into maps, either for single species or cumulatively for species assemblages, in order to assess conservation gaps between species needs and available areas. Another option is to compare and rank alternative management scenarios, as is often done in PVAs (Bakker and Doak, 2009; Beissinger and Westphal, 1998; Franz et al., 2013; Lindenmayer and Possingham, 1996; McCarthy et al., 2003; Pe'er et al., 2013; Possingham et al., 1993). In all cases, it is imperative to assess and discuss the assumptions, and to communicate and visualize uncertainty when converting rough estimates of species’ needs into careful application into planning and policy. Finally, if knowledge translates into action, further monitoring is essential.

4.4. Toward a broader application of the MAR concept

An important message which emerges from this study is that MAR must be bound explicitly rather than implicitly by time. Acknowledging that extinction probability of any population increases with time (Pimm and Raven, 2000), PVAs utilize viability criteria that consider both a probability of extinction and a time horizon within which viability is sought, such as 5% probability in 100 years (Beissinger and McCullough, 2002; Burgman et al., 1993; Pe'er et al., 2013). Similarly, but more implicitly, empirical studies of occupancy are likely affected by the timeframe in which populations may have been isolated, e.g., due to landscape or climate changes. Accordingly, one should not simply define a

MAR, but instead define a “MAR-VT”: the minimum area required to achieve a viability threshold within a predefined time horizon.

The contribution of dispersal to population persistence in patchy environments sets hurdles to identifying the area requirement of species from empirical settings. Ecological models can aid in this context as powerful tools to disentangle tightly-linked processes in mosaic (and/or dynamic) landscapes (Schippers et al., 2009; Van Teeffelen et al., 2012). Here, lessons can be learned from the realms of the Minimum Viable Population concept, where separate measures are used when the viability of metapopulations is sought: e.g., through identifying the Minimum Viable Metapopulation (MVM; Hanski et al., 1996). Developing such an index for the MAR may serve as a promising lane in future use of the concept, but will certainly be more challenging because metapopulation viability will differ considerably for the same total area, depending on the spatial configuration and degree of connectivity of the sub-populations (Drechsler and Wissel, 1997; Frank and Wissel, 1998; Verboom et al., 2001).

Further expansion of the availability of MAR estimates can emerge from careful translation of individual area requirements into population level requirements (Dale et al., 1994; Hovestadt et al., 1991). However, preliminary assessment of the literature identified several sources of complexity that impede such a process. First, home range area varies among individuals and alters in size and overlap as a function of population density, habitat quality, availability and configuration (Hansbauer et al., 2006), species’ behaviour, and the period of observation (e.g. Hansbauer et al., 2008; Harris et al., 1990; Swihart and Slade, 1985). Only few studies quantified such functional relationships, especially between density and home-range size (see e.g. Jetz et al., 2004; Trewhella et al., 1988). Additionally, studies often confuse home ranges with territories, whereas obviously not all species are territorial, not all territories are kept at all times, and only a subset of the home range is defended. Furthermore, densities change as a function of habitat quality (van Aarde and Jackson, 2007), heterogeneity, environmental and demographic stochasticity, management, etc. (Pimm et al., 1988; Pimm and Redfearn, 1988). Therefore, we suggest great caution in using individual area requirements for assessing the MAR until the functional relations are better characterized.

4.5. A remaining gap between policy needs and what scientists provide

The abovementioned caveats may explain the potential reluctance of many authors to provide values that may be perceived as over-simplistic and thus potentially hampering the efforts to protect species. Especially, threshold values such as the MAR may not reflect the functioning of populations, species and ecosystems. Yet the scarcity of application of this concept yields a discrepancy between policy needs and the outputs of scientific investigations. Inconsistent terminology and means to provide the MAR, combined with a multitude of viability measures, makes the outcomes of potentially-relevant studies both incomprehensive to decision-makers, and difficult to include in meta-analyses or other attempts to generalize. At the same time, simple means for communicating conservation needs are important for directing conservation policy and management. Therefore, the applicability of the MAR concept can be enhanced by identifying how it correlates to other viability measures (such as the MVP); obtaining better understanding of the impacts of population density on area usage; assessing the best scales of applicability; and examining circumstances where it can effectively feed statistical tools, simulation models (see e.g. Pereira et al., 2004) or other decision-support tools. To ensure that MAR estimates from focal (species-specific) studies aid biodiversity conservation, reliable data are needed on the habitat preferences, area requirements and movement capacities for a range of species. This requires efforts to

collect such data, yet it also requires greater awareness to the importance of comprehensive and standardized reporting in facilitating analyses across species and taxa (Pe'er et al., 2013; Schmolke et al., 2010). Online databases provide a more solid basis for data sharing and usage, and facilitate the capacity for common learning and application into applied conservation questions (Costello, 2013). Our MAR database is therefore available online (<http://www.scales.ckff.si/scaletool>). We encourage comments and contributions to the database, and stand ready to support attempts for its implementation into specific case studies or meta-analyses.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.biocon.2013.12.011>.

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