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Title: Species-area uncertainties impact the setting of habitat conservation targets and propagate across conservation solutions

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1 **1. Introduction**

2 Human domination of the natural world is resulting in biodiversity losses similar to those during
3 mass-extinction events recorded over geological time (Ceballos et al., 2017). In the marine realm,
4 biodiversity is threatened by numerous anthropogenic stressors, such as overfishing (Pauly et al.,
5 1998), climate change (Cheung et al., 2009) and biological invasions (Simberloff et al., 2013). In
6 this context, marine protected areas (MPAs) are promoted as tools to help conserve biodiversity
7 heritage (Wood et al., 2008), maintain ecosystem processes (Roberts et al., 2005), and favour a
8 sustainable exploitation of living resources (Agardy et al., 2003; Spalding et al., 2008).
9 Systematic Conservation Planning (SCP; Margules & Pressey, 2000) is a widely-used approach to
10 develop networks of protected areas. Based on the principle of complementarity, this approach
11 selects protected area systems that optimize the representation of each biodiversity feature occurring
12 in a region (e.g. species, habitats, ecosystem services ; Possingham et al., 2000; Carwardine et al.,
13 2009). A crucial step in the SCP process is to set conservation targets for biodiversity features.
14 These targets are explicit goals that quantify the minimum amount of each biodiversity feature to be
15 covered by the protected areas (Ball et al., 2009).
16 At the international level, the parties to the Convention on Biological Diversity (CBD) agreed in
17 2010 to protect 10% of their marine exclusive economic zone and 17% of their terrestrial lands and
18 inland waters by 2020 (Aichi Biodiversity Target n°11; CBD, 2010). These targets, expressed as
19 percentages of broad geographical regions are often translated in the SCP process as uniform
20 conservation targets such as 10% for each habitat type occurring in a region (Barr et al. 2011;
21 Pressey et al. 2003). Setting such uniform targets assumes that all habitats need to be equally
22 protected, and ignores biological variations across regions and habitats (Agardy et al., 2003; Pressey
23 et al., 2003). Moreover, the broadscale Aichi targets have been negotiated to encompass countries
24 with remarkably different economic, political and cultural backgrounds (Amengual & Alvarez-
25 Berastegui, 2018), and have been thus criticized for being justified in terms of political expediency
26 and for their lack of scientific background (Carwardine et al., 2009; Noss et al., 2012; Svancara et
27 al., 2005; Müller et al, 2018). In the marine realm particularly, a meta-analysis of published MPAs
28 networks concludes that the 10% marine target proves insufficient to meet many conservation goals,
29 such as the protection of biodiversity, has socio-economic limitations and does not account for the
30 connectivity within MPAs networks (O’Leary et al., 2016). Considering environmental and
31 biological variations by determining habitat-specific conservation targets has thus been advocated
32 to provide ecologically realistic and relevant conservation solutions (Wood, 2011; Woodley et al.,
33 2012).

34 The methodological strategy used for setting conservation targets varies according to the
35 biodiversity feature considered (Metcalf et al., 2013). When the biodiversity features are different
36 habitats occurring in the planning region, an extensively used approach to set habitat-specific
37 conservation targets is based on the Species-Area Relationship (SAR; Fig. 1 ; Rosenzweig, 1995;
38 Triantis et al., 2012). Building on the relationship between species richness and area (SAR), habitat-
39 specific conservation targets are set by estimating the proportion of a habitat required to represent a
40 given proportion of the total number of species occurring within it (step 2 Fig. 1 and for instance
41 Desmet & Cowling, 2004; Reyers et al., 2007; Metcalfe et al., 2013; Davis et al., 2017). These
42 habitat-specific conservation targets are then used to constrain the SCP reserve selection algorithm
43 when designing protected area networks (step 3 Fig. 1).

44 SARs are both universal and versatile. Positive relationships between species-richness and area
45 have been described for a wide variety of taxa, ranging from bacteria (Horner-Devine et al., 2004)
46 to vertebrates (Newmark et al., 2017), including invertebrates and plants (Triantis et al., 2012), as
47 well as for a variety of ecosystems and geographic locations (Adams et al., 2017; Deane et al.,
48 2017). Despite the universality of the pattern, systematic variations in the shape of SARs have been
49 reported across taxa and ecosystems. For example, Qian et al. (2007) identified a strong decrease in
50 the slope of SARs with increasing latitude for vascular plants in North America; and SARs have
51 been shown to vary in shape among taxa (Guilhaumon et al., 2008). The shape of SARs varies also
52 with scale, changing from exponential for small sampling areas to Power-law for intermediate
53 sampling areas, and sigmoid when representing entire biogeographical regions (He & Legendre,
54 1996); or depends on the method used to construct them (Scheiner, 2003).

55 Reflecting the variety of observed SAR shapes and the large body of theoretical work that interprets
56 the patterns, over 20 mathematical models have been developed to describe SARs (Tjørve, 2003,
57 2009). Although no agreement has been reached on a single and universal model (Connor and
58 McCoy 1979; Veech 2000; Fattorini 2007; Guilhaumon et al. 2008), the Power-law model
59 (Arrhenius, 1921) is often assumed to describe SARs well and is therefore the most widely used in
60 ecology and conservation science (Smith, 2010). For analytical convenience, simple linear
61 regression models obtained by log-transforming the Power-law equation are generally used in
62 conservation applications (see equations 1-3 in methods). When setting habitat conservation targets
63 using SARs, most studies do not even fit the log-transformed Power-law model to data, but instead
64 estimate the Power model parameters (and derive corresponding conservation targets) for a given
65 habitat on the basis of two data points (P_1, P_2): P_1 (x_1 = log of average area of sampling units, y_1 = log
66 of average number of species per sampling unit) and P_2 (x_2 = log of the total habitat area, y_2 = log of
67 the total number of species) (see methods for details, Desmet & Cowling, 2004; Rouget et al., 2004;

68 Metcalfe et al., 2013; Davis et al., 2017). Even though this approach (called hereafter the ‘*log-*
69 *transformed model*’) is more ecologically relevant than setting uniform conservation targets (e.g.
70 the 10% target adopted internationally) and may be useful in data-poor situations, it is not suited to
71 take into account the wide range of SAR shapes encountered across ecological conditions and
72 habitats. Consequently, when the *a priori* chosen model (e.g. *log-transformed model*) is
73 inappropriate for fitting the SAR, the estimation of conservation targets may potentially be
74 inaccurate and lead to inefficient reserve networks, in particular when the derived targets are less
75 ambitious than those estimated using the data-driven best fit. Conversely, when the *a priori* chosen
76 model estimates too ambitious targets, scarce conservation effort could be mismanaged, while it
77 could be rather used to protect more depleted habitats. Also, several SAR models could provide
78 equivalent good fits to empirical data sets, resulting in model-selection uncertainty. In such
79 situations, the choice of a particular SAR model to calculate conservation targets is delicate,
80 especially when the estimated habitat targets vary among good fits. Several studies have reported an
81 uncertainty when selecting the best SAR model for a given data set (Stiles & Scheiner, 2007;
82 Guilhaumon et al., 2008), with significant influence on the outcomes of a variety of ecological
83 applications, such as detecting richness hotspots (Guilhaumon et al., 2008) or estimating species
84 extinction rates (Matthews et al., 2014). For coping with SAR uncertainties, multi-model inference
85 has been recommended as a solution to provide a robust final inference, weighting several models
86 fits with respect to their relative probabilities to best fit the SAR (Step 2 Fig. 1 ; Grace et al., 2010;
87 Guilhaumon et al., 2008, 2010; Smith, 2010; Scheiner et al., 2011).

88 In this study, we investigate whether the uncertainty in the selection of SAR models propagates
89 throughout the entire SCP process and leads to different habitat targets and conservation solutions.
90 Using fishes of the coastal Mediterranean Sea as a case study, we aimed to answer the following
91 questions: (1) What are the uncertainties underlying the selection of SAR models for different
92 Mediterranean coastal marine habitats? We constructed empirical SARs for six Mediterranean
93 coastal marine habitats and compared in a model selection framework 20 SAR models (hereafter
94 SAR scenarios) to fit these empirical SARs. (2) Do SAR scenarios lead to different habitat
95 conservation targets, and do they propagate in the SCP process, resulting in distinct conservation
96 solutions? For each SAR scenario, we calculated conservation targets for the different habitats and
97 identified corresponding conservation solution using a reserve-selection algorithm. We then tested
98 whether dissimilarities between conservation targets estimated by different SAR models were
99 correlated to dissimilarities between the corresponding conservation solutions. (3) Finally, we asked
100 whether conservation targets and conservation solutions generated by taking into account SAR
101 uncertainties (i.e. using a multi-model inference) were different from those based on the *log-*

102 *transformed model?* We estimated conservation targets and associated conservation solutions using
103 both methods and analysed differences in conservation outcomes.

105 **2. Material and methods**

106 **2.1. Data**

107 Spatial distribution data for 635 Mediterranean fish species, which represent the entire
108 Mediterranean fish assemblage, were obtained as rasters at 0.1° resolution from the FishMed
109 database (Albouy et al., 2015). Raster maps for 6 Mediterranean Sea marine habitats, mainly coastal
110 (i.e. rocky reef, shallow soft, soft slope, soft shelf, seagrass and rocky intertidal; Fig. A1, Table 1),
111 based on the distribution of substrate types (e.g. soft, hard) and three depth ranges (shallow for 0-60
112 m, shelf for 60-200 m and slope for 200-2000 m), were obtained from Micheli et al. (2013) at 1km²
113 resolution (see Halpern et al, 2008 and Micheli et al, 2013 for further details), and resampled on the
114 species distribution grid.

115 **2.2. Species-area sampling**

116 Using gridded species distributions, we constructed empirical SAR for each habitat by tallying both
117 the number of species and the habitat surface area occurring at increasing levels of cells number
118 (step 1 Fig.1). For each level of n cells number (n ranging from 1 to N-1 grid cell, with N the total
119 number of grid cells observed in the focal habitat, and using a step of one grid cell), we sampled
120 randomly 100 sets of cells and averaged species richness and habitat surface area over these 100
121 sets, constructing empirical species-area curves of type IIB as defined by Scheiner (2003). For the
122 last level of N cells we used the total number of species observed in the focal habitat, without
123 replications.

124 When constructing empirical SARs, species are usually counted at the first encounter and
125 considered present at a given level of area even if they are represented by a single individual (He &
126 Hubbell, 2011). For conservation purposes, this approach would hardly promote the maintenance of
127 populations that are sufficiently viable to ensure species persistence. To address this limitation, we
128 considered that a species was present at a given level of area only if at least 10% of the species'
129 total range in the habitat considered was encompassed. This 10% coverage threshold was chosen
130 conservatively to allow for species persistence (Rodrigues et al., 2004; Venter et al., 2014;
131 Guilhaumon et al., 2015; Mouillot et al., 2016).

132 **2.3. Species-area modeling**

133 Many functional forms have been proposed to fit SARs; they differ in shape (e.g. convex, sigmoid,
134 asymptotic, non-asymptotic) and in the complexity of the corresponding mathematical model
135 (Triantis et al., 2012). For each habitat, we fitted 20 SAR models $\hat{S}_i = g_i(A)$, $1 \leq i \leq 20$ where \hat{S}_i is

136 the species richness inferred by model i for the habitat area A and g_i is the functional form,
137 including a linear function, nine convex functions and ten sigmoid functions, thus encompassing the
138 various SAR shapes gathered in the literature (Table 2). To compare the goodness-of-fit of SAR
139 models, we used the version of Akaike's Information Criterion (AICc; Akaike, 1987) corrected for
140 small samples. Model selection using AICc considers both fit and complexity when comparing
141 several models. We used Akaike weights (ω_i) derived from AICc values to reflect the probability of
142 each model to be the best in explaining the data (Burnham & Anderson, 2003). When the best-fitted
143 model has an Akaike weight greater than 0.9, robust inferences can be made using only this model;
144 however if none of the models has a weight greater than 0.9, no conclusion can be drawn about the
145 best model, reflecting a substantial uncertainty surrounding the model selection (Burnham &
146 Anderson, 2003). If so, model averaging has been recommended to make robust SAR predictions
147 (Guilhaumon et al., 2008). Here we performed multi-model inference by averaging SAR inferences
148 across models and weighting according to Akaike-weights : $\bar{S} = \sum_i \hat{S}_i \omega_i$.
149 All SAR analyses were conducted using an updated version of the R package "mmSAR"
150 (Guilhaumon et al., 2010), which estimates non-linear model parameters for numerous SAR
151 functional forms (Triantis et al., 2012). Of the 20 SAR models initially fitted, those with negative
152 R^2 (i.e. the model does not follow the trend of the data and fits worse than an intercept-only linear
153 regression) and those yielding negative predictions or a decrease in species richness with increasing
154 area were discarded. The remaining models differed by habitat, but for comparison purposes, only
155 the 13 models validated for all habitats were used to evaluate the sensitivity of the SCP process to
156 the selection of the SAR model (Table 2). We used an R^2 measure that compares the deviance of the
157 non linear SAR model with the deviance of a linear intercept-only model (Kvålseth, 1985) and used
158 these R^2 values as indicators of the proportion of the total variation in species richness that is
159 explained (accounted for) by the non linear SAR models.

160

161 **2.4. Conservation targets**

162 For a given habitat, targets were expressed as the proportion of that habitat area required to
163 represent a given proportion of the total number of species occurring within it. The proportion of
164 species is generally set at 70-80% (Desmet & Cowling, 2004; Metcalfe et al., 2013; Davis et al.,
165 2017). In this study, habitat targets were calculated to protect 80% of the fish fauna of each habitat.
166 For the six habitats, 13 fitting SARs models ($\hat{S} = g(A)$; Table 2) were used to derive the habitat-
167 target area A_t corresponding to 80% of the species richness (S_t) inferred for the total area of the

168 focal habitat ($S_{A_{tot}}^{\wedge}$). We also used multi-model inference for each habitat to estimate corresponding
169 conservation targets.

170 In addition, we calculated habitat targets following the *log-transformed model* approach developed
171 in Desmet & Cowling (2004), based on simplifications of the logarithmic transformation of the
172 Power-law model (Eq.1 and Eq.2 ; Arrhenius, 1921):

$$173 \hat{S} = cA^z \quad (1)$$

$$174 \log(\hat{S}) = c + z\log(A) \quad (2)$$

175 where \hat{S} = species richness, A = habitat area, z = the rate at which new species are encountered in a
176 system (Lomolino, 2000) and c is a scaling factor that relates to the area of an individual sampling
177 unit, which can be ignored when comparing percentages of species and area (Rondinini & Chiozza,
178 2010). The habitat-specific z-parameter was calculated using Eq. (3) as the slope of the *log-*
179 *transformed model* (Eq. 2).

$$180 z = (y_2 - y_1)/(x_2 - x_1) \quad (3)$$

181 where $y_2 = \log$ (total number of species in a habitat class), $y_1 = \log$ (mean number of species per
182 sampling point), $x_2 = \log$ (total area of the habitat class) and $x_1 = \log$ (mean area of sampling
183 points). Habitat-target area (A_t) was then calculated to protect $S_t = 80\%$ of predicted species
184 richness using equation 4 (Desmet & Cowling, 2004; Metcalfe et al., 2013).

$$185 \log(A_t) = \log(S_t)/z \quad (4)$$

186 **2.5. Systematic conservation planning**

187 We used the reserve-selection algorithm in the Marxan decision support tool (Ball et al., 2009) to
188 assess the implications of considering habitat-targets from different SAR scenarios on spatial
189 conservation solutions. Marxan uses a heuristic algorithm to minimize the opportunity cost (surface
190 area or socio-economic cost) of the set of Planning Units (PUs, here grid cells) selected as a
191 protected area system while ensuring predefined representativeness for each conservation feature
192 (here SARs habitat-targets). Near-optimal conservation solutions are generated by minimizing an
193 *objective function*, linear combination of three components: (1) total cost of the solution (sum of the
194 opportunity costs of the PUs selected in a given solution); (2) penalty associated with the spatial
195 compactness level of the solution, calibrated using a Boundary Length Modifier (BLM) and (3) sum
196 of Features Penalty Factor (FPF), which represents a penalty cost for each unmet target.

197 Because the value of the FPF and the BLM depend on the magnitude of conservation targets, it is
198 necessary to adjust, for each SAR scenario independently, the weights in the *objective function*
199 components (i.e. BLM and FPF) to be of similar magnitude, thus preventing any component from
200 outweighing the others (Stewart & Possingham, 2005; Ardron et al., 2008). Here we conducted

201 analyses without using BLM to allow comparison of conservation solutions based on different
202 SARs habitat-targets. FPF was incrementally increased for each habitat separately until all the
203 habitats would meet their SAR targets. We allocated an equal cost (set to 1) to the 15,539 PUs of
204 the planning region, as our aim was to examine differences in the selection of priority areas among
205 the SAR scenarios and not to design a cost-effective MPA network. We ran Marxan to identify a set
206 of 100 potential MPAs network solutions for each of the 15 SAR scenarios (13 fitting non-linear
207 SARs models, the *log-transformed model* and the SAR multi-model inference) using 1,000,000
208 iterations that were necessary for the heuristic algorithm to achieve near-optimal solutions. We then
209 calculated the “irreplaceability” value for each PU as the percentage of solutions that contained the
210 PU. The irreplaceability values emphasize the importance of each PU for achieving conservation
211 targets (Carwardine et al., 2007).

212 To emphasize the sensitivity of conservation planning to various SAR scenarios, we used two
213 different metrics. We first investigated the spatial overlap between the best conservation solutions
214 arising from the 13 different SAR scenarios (i.e. fitting non-linear SARs models). As such, PUs
215 were identified as priority areas of the least investment risk when selected among all models, or as
216 unsure for conservation plans when their selection depended on the SAR scenario. Second, we
217 derived pairwise comparisons between the 13 SAR scenarios by calculating, for each PU, the
218 difference in irreplaceability. We additionally defined the PUs selected across more than 50% of
219 conservation solutions as “highly irreplaceable” (and essential to effectively meet conservation
220 objectives (Ardron et al., 2008)), and compared them across SAR scenarios. The same analyses
221 were conducted to compare match and mismatches between the multi-model inference and the *log-*
222 *transformed model*, the relationship between respective PUs irreplaceability values was projected
223 onto an RGB (Red-Green-Blue) two-dimensional color space and mapped geographically.

224 **2.6. Uncertainty propagation analysis**

225 We used the Mantel test (Mantel, 1967) to test for a relationship between dissimilarities in
226 conservation targets and dissimilarities in conservation solutions arising from different SAR
227 models. In the Mantel test, a coefficient of correlation is computed between the two observed
228 dissimilarity matrices and its significance is evaluated by re-calculating the correlation after many
229 random permutations of the rows and columns of one dissimilarity matrix. We calculated the
230 dissimilarity between all pairs of habitat targets for the 13 fitting SAR models using Euclidean
231 distances. A second dissimilarity matrix between the same models was calculated on the basis of
232 PU irreplaceability values, using Euclidean distances as well. A strong and significant Mantel
233 correlation indicates that the dissimilarity in habitat-targets between SARs models is tightly linked

234 to the dissimilarity in conservation solutions, revealing that SAR uncertainties spread across the full
235 SCP process.

236 To visualize the dissimilarities between conservation solutions arising from different SAR scenarios
237 we used Nonmetric Multi-Dimensional Scaling (NMDS). We used the function “metaMDS” of the
238 R package “vegan” (Oksanen et al., 2008). Besides, a k-means partitioning was performed on the
239 irreplaceability values for all SAR scenarios, and the resulting grouping was projected in the NMDS
240 space to highlight groupings of SAR scenarios that generated similar conservation solutions.

241 **3. Results**

242 **3.1. SAR modeling**

243 Coefficients of determination (R^2) for the 13 SAR models ranged widely across habitats (i.e. from 0
244 to 1 for the *gompertz* model for the soft slope and rocky intertidal habitats, respectively) and
245 explained on average *c.* 90% of the total variation in species richness (mean \pm standard deviation
246 (SD) = 0.88 ± 0.18) (Table 3). More complex sigmoid models (i.e. *weibull3* and *mmf*) generally
247 explained more variation in species richness than simpler non-asymptotic convex models. Akaike
248 weights varied greatly among models and habitats, and the data empirically supported between 1
249 and 6 models (i.e. Akaike weights > 0), depending on the habitat (Table 3). For two habitats (i.e.
250 shallow soft and rocky intertidal), model selection probabilities spread almost equally between the
251 *mmf* and *heleg* models. For the seagrass habitat, data provided empirical support for the Power-law
252 model and five sigmoid asymptotic models (i.e. *mmf*, *weibull3*, *weibull4*, *gompertz* and *heleg*),
253 indicating uncertainty in the selection of the best fitting model. As for the other habitats (i.e. rocky
254 reef, soft slope, and soft shelf), the *weibull4* model was selected without uncertainty (i.e. Akaike
255 weights > 0.9) as the best-fitting model.

256 **3.2. Conservation targets**

257 For a given habitat, conservation targets differed substantially among SAR models (Table 4). The
258 difference between the maximum and minimum conservation targets predicted by different SAR
259 models exceeded 30% for all habitats. For example, conservation targets for the soft shelf habitat
260 varied from *c.* 8% for the *gompertz* model to *c.* 38% for the *power* model. Similarly, a given model
261 provided varying conservation targets among habitats. For example, the *monod* model identified
262 targets ranging from 18% to 87%, depending on the habitat. Calculating the mean target for a given
263 SAR model across habitats revealed a relationship between target sizes and model characteristics:
264 non-asymptotic models generated the largest targets (i.e. 54% and 59% for the *koba* and *power*,
265 respectively), while convex models generated larger targets than sigmoid models (Table 4).
266

267 Multi-model inference, weighting all 13 SAR models, determined a consensual conservation target
268 ranging from 9-97% depending on the habitat ($38\% \pm 35.5$) whereas the *log-transformed model*
269 yielded relatively less ambitious targets, ranging between 12-40% among habitats ($21\% \pm 9.7$). The
270 differences between the conservation targets estimated by these two methods can exceed 40% when
271 the multi-model inference generated the most ambitious targets (i.e. seagrass and rocky reef
272 habitats). Otherwise, targets estimated by the *log-transformed model* exceeded those estimated by
273 the multi-model by *c.* 8 % depending on the habitat (Table 3).

274 3.3 Conservation solutions

275 Although SAR scenarios that provided more ambitious targets ultimately led to more spatially
276 extensive conservation networks, conservation solutions for different SAR scenarios showed
277 different spatial distributions beyond their difference in size. While the less ambitious SAR scenario
278 (i.e. *gompertz*) provided an average target of *c.* 26% across habitats, consensual priority areas
279 among all SAR scenarios did not exceed 1% of the study area (Fig. 3 and Fig. A2): the PUs selected
280 by models estimating moderately ambitious targets were not necessarily selected by models that
281 estimate larger targets.

282 The spatial distribution of irreplaceability differed among SAR scenarios (Fig. 4). PUs that are
283 “highly irreplaceable” for achieving targets for a given SAR scenario are not likely to be so for
284 another SAR scenario. In all pairwise SAR scenarios comparisons, between *c.* 2%- 50% of “Highly
285 irreplaceable” PUs differed, while only *c.* 2% presented maximum irreplaceability across all SAR
286 scenarios (Fig. A3; Table A4).

287 The comparison between irreplaceability values for the multi-model SAR and the *log-transformed*
288 *model* revealed substantial differences over 10% of the study area (Fig. 5). Several patches of
289 “highly irreplaceable” PUs under the multi-model SAR scenario were spread across the Balearic
290 Islands (Spain), Sicily (Italy) and Corsica (France), covering mainly seagrass and rocky reef
291 habitats; irreplaceability values for the corresponding PUs under the *log-transformed model* were
292 systematically low.

293 3.4. SARs uncertainties propagation

294 A Mantel r-statistic of 0.97 (p-value=0.01) suggested a strong, positive and significant correlation
295 between SARs habitat-targets dissimilarities and conservation solutions dissimilarities, revealing
296 that differences in SARs inferences propagate through the SCP process and lead to different
297 conservation solutions. The two-dimensional NMDS (Fig. 6) produced high congruence between
298 the observed and ordinated distances (non-metric fit $R^2 = 0.99$) and a stress value of 0.02
299 distinguished clearly conservation solutions of the *log-transformed model* from other SAR
300 scenarios. A k-means clustering distinguishing five groups of SAR models partitioned the models

301 as follows. A first group of three non-asymptotic models (*power*, *koba* and *P2*). A second group
302 gathering four sigmoid asymptotic models (*weibull3*, *weibull4*, *heleg* and *mmf*) and the multi-model
303 inference. A third group including both convex asymptotic and sigmoid models with 2-3 parameters
304 (i.e. *monod*, *epm2*, *negexpo* and *chapman*) while the *gompertz* and *betap* models were aggregated
305 into a fourth group. The *log-transformed model* was isolated in a fifth group. Note that all models of
306 the second group were most frequently selected as the best models among habitats and that models
307 of the third group had null Akaike weights across all habitats (Table 3).

309 **4. Discussion**

310 As expected from the literature evidence, the shapes of coastal Mediterranean SARs varied greatly
311 among habitats, including convex, exponential and sigmoid tendencies (Fig. 2). The best fitting
312 SAR model differed by habitat and although the mean R^2 was relatively high, the goodness-of-fit of
313 the 13 models varied greatly among the six marine habitat types we considered. Hence, assuming
314 any of the numerous models described in the literature to provide an optimal fit for all the habitat
315 data sets analysed here would have led to spurious inferences (Smith, 2010). Indeed, our results
316 confirm that models that fit well for one habitat may not do so for other habitats (Connor & McCoy,
317 1979; Guilhaumon et al., 2008; Stiles & Scheiner, 2007; Triantis et al., 2012).

318 Furthermore, based on AICc weights, we detected a substantial uncertainty in the selection of the
319 best SAR model for three habitats, with several models (mostly sigmoid asymptotic) supported by
320 empirical SARs. For the other habitats, a sigmoid asymptotic model was selected as best-fitting
321 SAR (Table 3). Our findings of substantial support for sigmoid asymptotic SARs models for
322 Mediterranean habitats, would not be considered in classical analyses assuming *a priori* the Power-
323 law SAR or its *log-transformed model*. As pertaining from the versatility of the SAR, the
324 justification for particular SAR models is problematic in the literature, and when the data allows,
325 testing among existing SAR models is advocated (Smith et al., 2010; Scheiner et al., 2011; Davis et
326 al., 2017). Furthermore, when numerous models show equivalent support for empirical SARs,
327 testing a range of SARs models is prospectively essential to allow a multi-model inference robust to
328 the assumption of a particular SAR model (Burnham and Anderson, 2003).

329 The comparison of conservation habitat-targets revealed substantial differences among SAR
330 scenarios. For example, while the best-fitting model for soft shelf habitat (i.e. *weibull4*) predicted a
331 target of 13%, other models predicted markedly different ranges of targets (e.g. from 7% to 38% for
332 *gompertz* and *power* models, respectively). In general, for the threshold of 80% of species richness
333 coverage employed here, non-asymptotic models predicted the largest targets, and convex models

334 predicted larger targets than sigmoid models. The model used, whether convex or sigmoid or with
335 an asymptote, significantly influenced the amount of each habitat to be secured in protected areas.
336 Using multi-model inference resulted in a mean conservation target of *c.* 38% over the entire study
337 area. This conservation target, devised to protect 80% of the species within each habitat, as
338 recommended by international conservation institutions (Desmet & Cowling, 2004; Metcalfe et al.,
339 2013; Davis et al., 2017), and combined with the 10% coverage threshold to construct SARs,
340 promotes both species representation and persistence within each habitat. Accordingly, in the
341 Mediterranean Sea, the conservation target of 10% of the marine area set by the CBD (2010) would
342 leave some key habitats under-protected to represent 80% of the species (i.e. seagrass and rocky
343 reefs). Additionally, this result supports the recommendations of the 2014 World Parks Congress,
344 which called for protection of at least 30% of marine areas, as in previous studies (O’Leary et al.,
345 2016). On the other hand, the use of the *log-transformed model* is justified on the assumption that
346 the *power* model is the most appropriate at fitting all SAR datasets. However, our results show that
347 a *power* model, fitted as a non-linear regression by minimizing the residual sum of squares, was
348 never selected as the best fitting one, except for the seagrass habitat, where the *power* model holds a
349 share of the statistical information in explaining empirical SAR. If employed, habitat-conservation
350 targets estimated with the *log-transformed model* would provide insufficient protection level for
351 some key habitats in the life cycle of Mediterranean fish species (i.e. seagrass and rocky reef
352 habitats). On the flip side, when targets estimated with the *log-transformed model* exceeded those
353 estimated by the multi-model SAR, the protection of the corresponding habitats may be overstated,
354 leading to waste of scarce conservation resources that could be used to protect more needful
355 habitats. Overall, our investigations revealed strong differences in SAR scenarios on the setting of
356 habitat-specific conservation targets, with the *log-transformed model* providing conservation targets
357 diverging markedly from data-driven SAR inferences. As such, beyond providing ecologically
358 relevant conservation targets, considering habitat specificities by modeling empirical SARs is
359 relevant for a parsimonious allocation of conservation funds.

360 Importantly, beyond an effect on the magnitude of conservation targets, our study revealed that the
361 spatial distribution of selected priority areas depends on the SAR scenario used (Fig. 3, Fig. 4). As
362 shown here, conservation solutions for less ambitious targets are not always subsets of conservation
363 solutions for more ambitious targets (Fig. 3), confirming that the spatial distribution of conservation
364 solutions is target-specific (Margules & Pressey, 2000). Pairwise comparison between
365 irreplaceability values under different SAR scenarios revealed a maximal congruence of 50% of
366 ”highly irreplaceable” PUs (Fig.A3; Table A4). Our analyses highlighted that dissimilarities in
367 habitat-targets associated with alternative SAR scenarios propagate throughout the SCP process and

368 lead to correlated dissimilarities in conservation outcomes. This is of special concern given the wide
369 range of magnitude for targets estimated under different SAR scenarios (exceeding 30% for e.g.
370 rocky reefs or soft slopes; Table 4). The clustering of SAR scenarios in the NMDS based on
371 irreplaceability values (Fig. 6) shows that models with similar shapes were likely to generate similar
372 conservation solutions (e.g. the group of sigmoid models vs the group of convex models in Fig. 6).
373 This suggests the necessity to consider a wide range of SAR shapes when estimating habitat
374 conservation targets and solutions. On another note, the overlap among the 13 best conservation
375 solutions, each based on a different SAR scenario, revealed that priority areas of the least
376 investment risk (i.e. consensual areas among all SAR models) occupied only 1% of the total study
377 area. Most of these consensual PUs are already located in established MPAs (e.g. Cabrera National
378 Park (Spain), reserve of Lavezzi islands (France), Egadi MPA (Italy), MPA of “Penisola del Sinis -
379 Isola di Mal di Ventre” (Italy) and MPA of Ustica Island (Italy); Fig.5), indicating that the current
380 Mediterranean MPAs system provides a valuable starting point to establish a relevant conservation
381 network for coastal habitat conservation (Guilhaumon et al. 2015).

382 Comparing the multi-model SAR and the *log-transformed model*, SCP outcomes showed strong
383 effects of the method on the spatial distribution of irreplaceability values. Particular conservation
384 implications of using both methods can be highlighted by scrutinizing areas with larger differences
385 in irreplaceability values (Fig. 5). Most of these areas, such as the Balearic Islands in Spain, the
386 Gulf of Gabes in Tunisia, and the coasts of Sicily in Italy and Corsica in France, are predicted to be
387 irreplaceable under the multi-model SAR scenario but not by the *log-transformed model*. Some of
388 these priority areas overlap with established MPAs, while most are located in unprotected areas,
389 such as the Gulf of Gabes, known to be a shelter for one of the most extensive *Posidonia oceanica*
390 meadows in the Mediterranean sea (Batisse & Jeudy de Grissac, 1998) and a fish functional
391 diversity hotspot (Mouillot et al., 2011).

392 In conclusion, our findings highlight the potential consequences of the choice of a particular SAR
393 model on the different stages of habitat-based SCP. SAR uncertainties propagate through the SCP
394 process, confirming our theoretical anticipation that ignoring SARs specificities when setting
395 habitat conservation targets may lead either to a waste of resources limited by socio-economic
396 constraints or to the under-representation of biological conservation features. When the data allows,
397 a shift from an *a priori* defined SAR model or uniform targets towards a data-based approach would
398 provide stakeholders with better guidance on the appropriate strategies for habitats conservation.
399 Failing to do so may well lead to uncertain conservation outcomes, as exemplified herein the
400 identification of conservation plans among coastal Mediterranean habitats.

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Figure captions :

Figure 1 : Description of the different steps of the workflow for habitats conservation planning using Species-Area Relationships (SARs). Gray points indicate the empirical SAR and SAR scenarios are represented by solid lines. On each plot in *Step 2*, horizontal and vertical dashed lines indicate respectively the threshold of 80% of total predicted species richness and the corresponding habitat area to protect. In *Step 3*, the colors of the selected planning units correspond to the color of the scenario in *Step 2*.

Figure 2: Empirical (gray points) and fitted (lines) SAR for six Mediterranean coastal habitats : (a) rocky reef, (b) shallow soft, (c) soft slope, (d) soft shelf, (e) seagrass and (f) rocky intertidal. Model codes as in Table 1.

Figure 3: The overlap between the best conservation solutions under 13 SAR scenarios. The color of each planning unit indicate the number of SAR scenarios among which it was part of the best conservation solution. Locations of five marine protected areas : 1, Cabrera National Park ; 2, reserve of Lavezzi Islands ; 3, Egadi MPA ; 4, MPA of Ustica Island and 5, MPA of “Penisola del Sinis - Isola di Mal di Ventre”.

Figure 4: Irreplaceability values of planning units in the Mediterranean Sea under different SAR scenarios : (a) power , (b) epm2, (c) P2, (d) koba, (e) mmf, (f) monod. (g) negexpo, (h) chapman, (i) weibull3, (j) gompertz, (k) weibull4, (l) betap, (m) heleg (n) the *log-transformed model* and (o) the multi-model inference. Model codes as in Table 1.

Figure 5: Matches and mismatches between the multi-model inference and the *log-transformed model* SAR scenarios. Planning units colors are produced by projecting irreplaceability values within a two-dimensional RGB (Red-Green-Blue) color space as indicated in the inset.

Figure 6: Non-metric multi-dimensional scaling ordination of the irreplaceability values of SAR scenarios. Colors represent groups identified using a k-means clustering method. The point “multi-model” represents the multi-model inference, while “log-transform” indicates the *log-transformed model*.

Tables :

427 **Table 1:** Characteristics of six coastal habitat types in the Mediterranean Sea used in this study:
 428 total area, species richness, mean habitat area per planning unit (PU) and mean number of species
 429 per planning unit.

Habitat type	Area (km ²)	No. of species	No. of PUs	Mean habitat area per PU (km ²)	Mean no. of species per PU
Rocky reef	37689.248	576	837	45.02	207
Shallow soft	190334.881	595	4462	42.65	203
Soft slope	879488.256	589	11349	77.49	62
Soft shelf	225536.802	593	5304	42.52	168
Seagrass	3158.366	520	286	11.04	285
Rocky intertidal	18522.185	594	2844	6.51	229

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431 **Table 2:** The analytical formula, shape, presence/absence of an asymptote and number of
 432 parameters of the 20 models analyzed. S is species richness, A is the area, and c, d, f, and z are
 433 fitted parameters. Bold font identifies the 13 models selected for conservation planning analyses.

Model name	Code	Formula	Parameters	Shape	Asymptote?
Linear	linear	$S = c + zA$	2	Linear	×
Power	power	$S = cA^z$	2	Convex	×
Power Rosenzweig	power_R	$S = k + cA^z$	3	Convex	×
Extended power-law model 1	epm1	$S = cA^{zA-d}$	3	Sigmoid	×
Extended power-law model 2	epm2	$S = cA^{z-(c/A)}$	3	Sigmoid	×
Persistence function 1	P1	$S = cA^z e^{(-dA)}$	3	Convex	×
Persistence	P2	$S = cA^z e^{(-d/A)}$	3	Sigmoid	×

function 2					
Exponential	expo	$S = c + z \log A$	2	Convex	×
Kobayashi logarithmic	koba	$S = c \log(1 + A/z)$	2	Convex	×
Monod	monod	$S = d/(1 + cA^{-1})$	2	Convex	✓
Morgan- Mercer-Foldin	mmf	$S = d/(1 + cA^{-z})$	3	Sigmoid	✓
Logistic	heleg	$S = c/(f + A^{-z})$	3	Sigmoid	✓
Negative exponential	negexpo	$S = d(1 - e^{-zA})$	2	Convex	✓
Chapman- Richards	chapman	$S = d(1 - e^{-zA})^c$	3	Sigmoid	✓
Weibull 3	weibull3	$S = d(1 - e^{-cA^z})$	3	Sigmoid	✓
Weibull4	weibull4	$S = d(1 - e^{-cA^z})^f$	4	Sigmoid	✓
Asymptotic regression	asyp	$S = d - cz^A$	3	Convex	✓
Rational	ratio	$S = (c + zA)/(1 + dA)$	3	Convex	✓
Gompertz	gompertz	$S = de^{(-e^{-z(A-c)})}$	3	Sigmoid	✓
Beta-P	betap	$S = d[1 - (1 + (A/c)^z)^{-f}]$	4	Sigmoid	✓

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Table 3: Model selection and goodness-of-fit for 13 SAR models in six Mediterranean coastal habitats. R^2 is the coefficient of determination, AICc is the Akaike Information Criterion corrected for small samples and ω is Akaike model weight, which reflects the probability that a model is the best at fitting the data. Model codes as in Table 1.

<i>Model</i>	<i>Rocky reef</i>			<i>Shallow soft</i>			<i>Soft slope</i>			<i>Soft shelf</i>			<i>Seagrass</i>			<i>Rocky intertidal</i>		
	R^2	AICc	ω	R^2	AICc	ω	R^2	AICc	ω	R^2	AICc	ω	R^2	AICc	ω	R^2	AICc	ω
power	0.94	6 904	0	0.54	46 349	0	0.9	89 174	0	0.68	48 726	0	0.98	1 834	0.38	0.56	31 112	0
epm2	0.99	5 639	0	0.83	41 365	0	0.97	76 515	0	0.93	40 224	0	0.97	1 962	0	0.79	28 650	0
P2	0.99	5 453	0	0.85	40 712	0	0.9	89 178	0	0.94	39 011	0	0.98	1 849	0	0.82	28252	0
koba	0.94	6 919	0	0.63	45 245	0	0.95	82 590	0	0.77	46 830	0	0.86	2 529	0	0.65	30407	0
mmf	1	4 547	0	1	14 900	0.48	0.98	71 465	0	0.99	26 153	0	0.98	1 836	0.14	1	14581	0.50
monod	0.94	6 919	0	0.78	42 584	0	0.97	76 452	0	0.89	42 728	0	0.86	2 529	0	0.75	29287	0
negexpo	0.94	6 919	0	0.87	40 025	0	0.99	67 774	0	0.96	37 477	0	0.87	2 529	0	0.82	28207	0
chapman	0.94	6 921	0	0.87	40 027	0	0.98	72 379	0	0.96	37 479	0	0.86	2 532	0	0.82	28209	0
weibull3	0.99	4 961	0	1	19 295	0	0.99	64 386	0	1	20 227	0	0.98	1 836	0.14	1	15020	0
gompertz	0.81	8 000	0	0.06	49 994	0	0	115 925	0	0.76	47 084	0	0.98	1 836	0.13	1	15387	0
weibull4	1	4 466	1	1	16 235	0	1	40 626	1	1	20 182	1	0.98	1 838	0.05	1	15271	0
betap	0.99	4 963	0	0.99	23 323	0	0.51	107 688	0	0.79	46 424	0	0.9	2 425	0	1	14999	0
heleg	1	4 547	0	1	14 899	0.52	0.98	71 464	0	0.99	26 153	0	0.98	1 836	0.14	1	14581	0.50

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Table 4: Conservation targets, expressed as the percentage of each habitat required to protect 80% of species according to 13 non-linear SAR models, the *log-transformed model* and the multi-model SAR. Mean habitat targets for a given SAR model across habitats ; Mean habitat targets for a given habitat across SAR scenarios; ranges of targets estimated across SAR scenarios for each habitat (maximum minus minimum target).

	<i>Rocky reef</i>	<i>Shallow soft</i>	<i>Soft slope</i>	<i>Soft shelf</i>	<i>Seagrass</i>	<i>Rocky intertidal</i>	<i>Mean % target</i>
<i>power</i>	83.02	34.15	57.69	38.31	97.42	45.67	59.37
<i>epm2</i>	74.34	18.23	38.28	20.61	95.95	26.55	45.65
<i>P2</i>	73.06	17.18	57.69	19.49	97.27	24.85	48.25
<i>koba</i>	81.45	31.95	51	34.47	87.57	41.01	54.57
<i>mmf</i>	62.84	9.31	37.21	13.69	97.42	11.94	38.73
<i>monod</i>	81.45	18.47	43.63	21.77	87.57	26.92	46.63
<i>negexpo</i>	81.32	13.46	36.94	16.35	87.8	19.44	42.55
<i>chapman</i>	81.32	13.46	33.39	16.35	87.57	19.44	41.92
<i>weibull3</i>	61.36	9.34	34.17	13.82	97.42	11.77	37.98
<i>gompertz</i>	36.62	0.41	0.06	7.97	98.98	11.94	25.99
<i>weibull4</i>	64.13	9.37	33.35	13.82	97.42	11.94	38.33
<i>betap</i>	61.36	9.52	13.07	35.19	85.8	11.77	36.11
<i>heleg</i>	62.84	9.31	37.21	13.69	97.42	11.94	38.73
<i>Multi-model</i>	64.13	9.31	33.35	13.82	97.42	11.94	38.32
<i>Log-transformed model</i>	22.95	17.42	39.61	21.79	12.18	15.41	21.56
<i>Mean % target</i>	66.14	14.72	36.44	20.07	88.34	20.16	

% target range 60.07 33.73 57.62 30.33 86.80 33.89

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SUPPORTING INFORMATION

Figure A1: Habitat types in the Mediterranean Sea : (a) rocky reef, (b) shallow soft, (c) soft slope, (d) soft shelf, (e) seagrass and (f) rocky intertidal.

Figure A2 : Best solutions for each SAR scenario : (a) power , (b) epn2, (c) P2, (d) koba, (e) mmf, (f) monod. (g) negexpo, (h) chapman, (i) weibull3, (j) gompertz, (k) weibull4, (l) betap, (m) heleg, (n) the *log-transformed model* and (o) the multi-model inference. Model codes as in Table 1.

Figure A3 : Pairwise comparison of irreplaceability values of planning units under 13 SAR scenarios. Upper triangle illustrates differences in irreplaceability values between two given SAR scenarios. Colors of planning units in scatter plots (lower triangle) and maps indicate the differences in irreplaceability values between two SAR scenarios.

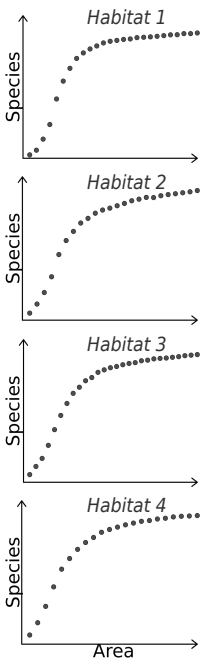
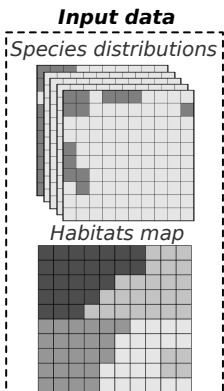
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Table A4 : Pairwise comparison of matches and mismatches of “highly irreplaceable” planning units under 13 SAR scenarios : The percentage of “highly irreplaceable” planning units selected under the SAR scenario and not under the other are given in upper triangle; the percentage of “highly irreplaceable” planning units selected under both SAR scenarios are represented in lower triangle.

<i>Model</i>	power	epm2	P2	koba	mmf	monod	negexpo	chapman	weibull3	gompertz
power		45.82	6.7	13.59	46.97	33.95	47.31	50.26	49.95	53.14
epm2	8.04		42.56	32.59	5.67	12.53	4.96	4.2	4.64	6.28
P2	49.16	18.33		14.32	43.45	30.96	44.06	47	46.43	49.62
koba	7.92	17.29	4.27		33.77	22.87	33.66	36.42	36.41	39.49
mmf	39.78	5.68	4.37	4.07		13.55	5.01	4.25	3.78	5.22
monod	7.74	6.72	3.52	3.64	1.64		13	14.42	14.8	17.25
negexpo	37.75	4.73	4.25	3.31	1.63	3.9		3.1	3.84	5.22
chapman	6.98	6.6	3.95	1.79	1.87	3.55	3.13		2.28	2.92
weibull3	4.49	6.63	4.56	1.78	4.25	3.34	3.19	3.08		2.79
gompertz	7	4.18	3.86	1.8	3.79	3.54	3.08	1.61	7.1	
weibull4	6.64	5.9	4.56	1.67	4.26	1.78	3.11	3.09	6.76	4.12
betap	18.64	4.4	4.38	1.78	4.08	3.24	3.1	7.1	4.38	3.48
heleg	6.73	4.05	3.82	1.65	3.69	3.13	3.08	4.49	5.71	3.78

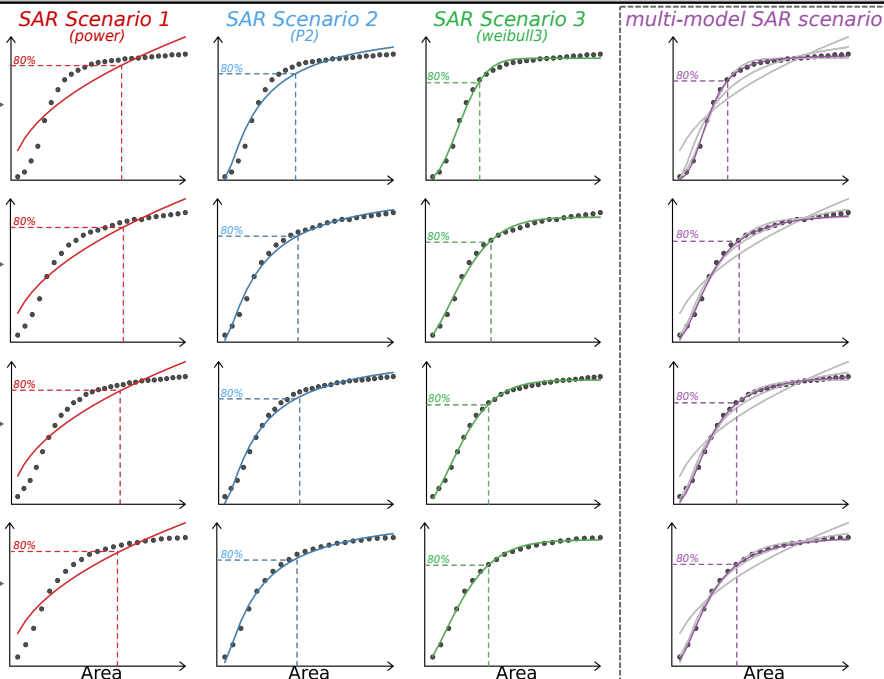
Step 1 : Empirical SARs

Species richness and habitat area are tallied for increasing surface level (number of planning units) for each habitat of study area.



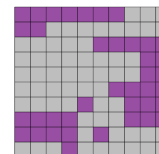
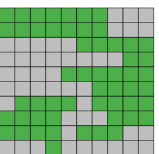
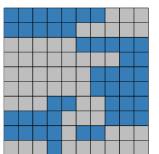
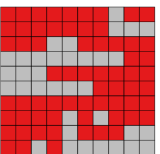
Step 2 : SAR models and conservation targets

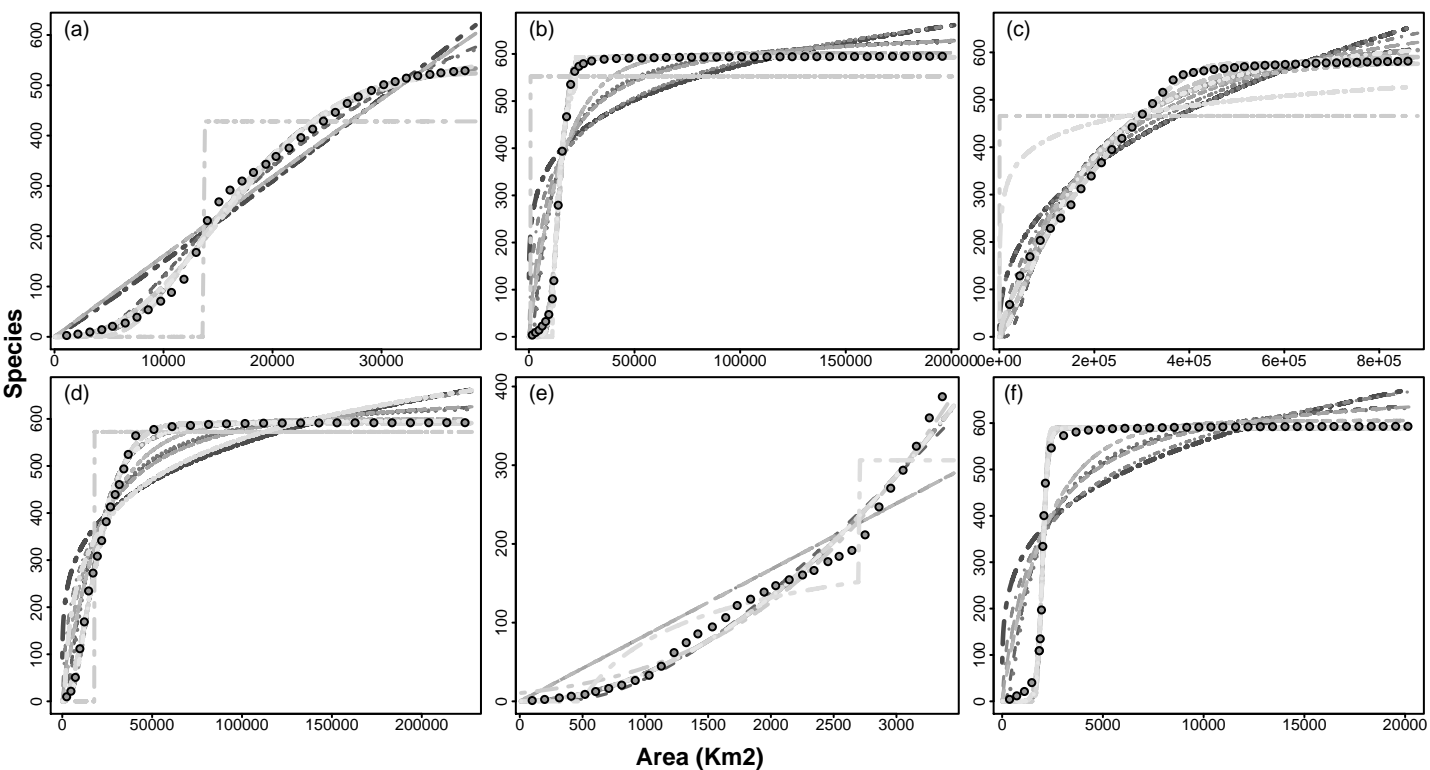
For each habitat, the empirical SAR is fitted according to different SAR scenarios (here 3 SAR models and a multi-model inference). The corresponding conservation targets are then inferred to protect a given percentage (here 80%) of the total species richness of each habitat.



Step 3: Conservation planning

A reserve-selection algorithm (here Marxan) is used to generate a conservation solution based on each SAR scenario.





—	power	- · - ·	koba	- - -	negexpo	- - -	gompertz	- - -	heleg
- - -	epm2	- - -	mmf	- - -	chapman	- - -	weibull4		
· · ·	P2	- - -	monod	- - -	weibull3	- - -	betap		

