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1 **Model development for the assessment of terrestrial and aquatic**
2 **habitat quality in conservation planning**

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21 **Abstract**

22 There is a growing pressure of human activities on natural habitats, which leads to
23 biodiversity losses. To mitigate the impact of human activities, environmental policies are
24 developed and implemented, but their effects are commonly not well understood because
25 of the lack of tools to predict the effects of conservation policies on habitat quality and/or
26 diversity. We present a straightforward model for the simultaneous assessment of terrestrial
27 and aquatic habitat quality in river basins as a function of land use and anthropogenic
28 threats to habitat that could be applied under different management scenarios to help
29 understand the trade-offs of conservation actions. We modify the InVEST model for the
30 assessment of terrestrial habitat quality and extend it to freshwater habitats. We assess the
31 model reliability in a severely impaired basin by comparing modeled results to observed
32 terrestrial and aquatic biodiversity data. Estimated habitat quality is significantly correlated
33 with observed terrestrial vascular plant richness ($R^2 = 0.76$) and diversity of aquatic
34 macroinvertebrates ($R^2 = 0.34$), as well as with ecosystem functions such as in-stream
35 phosphorus retention ($R^2 = 0.45$). After that, we analyze different scenarios to assess the
36 model suitability to inform changes in habitat quality under different conservation strategies.
37 We believe that the developed model can be useful to assess potential levels of
38 biodiversity, and to support conservation planning given its capacity to forecast the effects
39 of management actions in river basins.

40

41 **Keywords:** anthropogenic threats; biodiversity; environmental management; habitat quality;
42 scenario analysis; river basin.

43

44 **1. Introduction**

45 Loss and degradation of natural habitats is a primary cause of declining biodiversity (Fuller
46 et al., 2007), yet humans must balance conservation with development needs. It is difficult
47 to strike such a balance with inadequate information about the consequences of our land
48 use and management decisions. Nevertheless, we do know that the main drivers of the
49 decrease in habitat quality are land use and climate change (Sala et al., 2000), which are
50 exacerbated by other anthropogenic threats such as the construction of infrastructure and
51 the introduction of exotic species (Ricciardi and Rasmussen, 1999). Worldwide, species
52 extinction in freshwater environments is estimated to be higher than in terrestrial
53 ecosystems (McAllister et al., 1997; Abell, 2002). Despite their reduced extent, freshwater
54 systems support 10% of all known species (Carrizo et al., 2013). One of the reasons for
55 higher extinction rates in freshwater is the difficulty of conservation efforts. Freshwater
56 systems are susceptible not only to direct impacts but also to indirect impacts from
57 disturbances elsewhere in the basin, all of which can contribute to the loss of biodiversity in
58 rivers. Whereas many terrestrial conservation programs consider only threats adjacent to
59 the site of interest, conservation of freshwater systems needs to take into account the
60 connected nature of rivers, which present a strong directional component (Ward et al.,
61 2002; Moilanen et al., 2008; Linke et al., 2011).

62 Maintaining and protecting habitat quality and biodiversity, while still meeting human needs,
63 is an urgent task in ecosystems management. Efforts to preserve biodiversity have resulted
64 in the creation of a variety of environmental policies, like the ambitious new strategy
65 adopted in 2012 by the European Parliament to halt the loss of biodiversity and ecosystem
66 services in the European Union (EU) by year 2020, or the USA Endangered Species Act of
67 1973, and the Fish and Wildlife Conservation Act of 1980 (Goble et al., 2005; Stoms et al.,
68 2010; EC, 2011). Other laws are oriented to restoring and maintaining the biological
69 integrity of freshwater ecosystems, such as the Water Framework Directive of year 2000 in
70 the EU, or the Clean Water Act of 1965 in the USA (Karr, 1991; Griffiths, 2002). Major

71 conservation efforts also exist in emerging economies such as China, which committed to
72 setting aside 23% of the country as priority conservation areas through the Strategy and
73 Action Plan for Biodiversity Conservation of 2010 (MEPC, 2011). Similarly, some Latin
74 American countries have progressive conservation policies, like Costa Rica's Biodiversity
75 Law of 1998 and Colombia's National System of Protected Areas of 2010 (Solís-Rivera and
76 Madrigal-Cordero, 1999; Vasquez and Serrano, 2009).

77 Environmental policies should go along with further understanding of the necessary actions
78 to preserve habitats and species (Strayer and Dudgeon, 2010). Scenario analysis has
79 proved useful for assessing the effects of specific management actions on biodiversity
80 (Kass et al., 2011; Nelson et al., 2011; Carwardine et al., 2012), identifying vulnerability to
81 global change (Pereira et al., 2010; Domisch et al., 2013), and guiding conservation
82 planning (Dauwalter and Rahel, 2008; Hermoso et al., 2011; Moilanen et al., 2011). Thus,
83 central to any conservation strategy throughout the world has been the establishment of
84 protected areas, which has led to the evolvement of the systematic conservation planning.
85 Regarding this, systematic conservation tools have been designed to help planners decide
86 on the location and configuration of conservation areas, so that the biodiversity value of
87 each area can be maximized. Among these tools we find models like Marxan (Ball et al.,
88 2009), Zonation (Moilanen et al., 2009), C-Plan (Pressey et al., 2009) or ConsNet (Sarkar
89 et al., 2006). Recent conservation efforts have also used species distribution models to
90 deliver insights on the relationship between biodiversity and the environment (Elith and
91 Leathwick, 2009; Vander Laan et al., 2013; Kuemmerlen et al., 2014). These models
92 usually relate known occurrences of a species with environmental conditions and predict
93 occurrences in areas where suitable environmental conditions are known but no occurrence
94 data is available. More recently, focus has shifted towards understanding and incorporating
95 the distribution of threats (Allan et al., 2013; Tulloch et al., 2015). Approaches to threat
96 mapping range from mapping the distribution of a single threat to additive scoring
97 approaches for multiple threats that incorporate ecosystem vulnerability (Evans et al., 2011;

98 Coll et al., 2012; Auerbach et al., 2014). Models that predict the status of biodiversity as a
99 function of anthropogenic threats using biodiversity proxies are useful to inform
100 management. Such models include GLOBIO (Alkemade et al., 2009) and InVEST
101 (*Integrated Valuation of Environmental Services and Tradeoffs*; Tallis et al., 2011; Sharp et
102 al., 2014), that are based on the mean species abundance (MSA) and on estimates of
103 habitat quality respectively. However, proxy effectiveness as adequate indicator of
104 biodiversity has not been fully tested (Eigenbrod et al., 2010), and this can only be achieved
105 by rigorous comparison of biodiversity proxies such as habitat quality to different indicators
106 of biodiversity (either species richness, taxa, rarity, etc.) over space and time. Unlike
107 GLOBIO, that uses a biodiversity index related to a baseline corresponding to the similarity
108 to the natural situation, InVEST requires to assess which habitat type reflects natural
109 conditions the best. The InVEST habitat quality model has successfully been applied to
110 estimate the impact of different scenarios of land use / land cover (LU/LC) change or
111 conservation policies on terrestrial habitat for biodiversity (Polasky et al., 2011; Bai et al.,
112 2011; Nelson et al., 2011; Leh et al., 2013; Baral et al., 2014). Since InVEST is by now
113 exclusively estimating the habitat quality of terrestrial ecosystems, developing tools that
114 include the aquatic compartment together with the terrestrial is highly advisable given the
115 increasing concern for freshwater biota and the interrelation of the two compartments. Both
116 terrestrial and aquatic components play an important role in environmental management for
117 habitat protection (Palmer et al., 2008).

118 In this study, we adapt the deterministic spatially-explicit habitat quality module of the
119 InVEST suite of models for the assessment of habitat quality in river basins, considering the
120 effects of anthropogenic threats on terrestrial and aquatic habitat. The extension of the
121 module to assess aquatic ecosystems is one of the improvements presented in this work.
122 Our goal is to provide a simple model that can be used to reliably assess the effects of
123 ongoing threats and environmental management actions on habitat quality and current
124 levels of biodiversity, and that allows for scenario analysis in order to forecast the effects of

125 future management actions. We select the InVEST model because it proceeds with data on
126 LU/LC, anthropogenic threats and expert knowledge, to obtain reliable indicators about the
127 current and future response of biodiversity to threats, and because unlike other approaches
128 used in biodiversity conservation, it does not require prior information about the distribution
129 or presence of species. To illustrate the model performance, we apply it to the case study of
130 a severely impaired basin in the Mediterranean region (Llobregat River basin, NE Iberian
131 Peninsula). We test the model reliability by comparing the estimated habitat quality values
132 with observed terrestrial and aquatic biodiversity data. We also check the response of the
133 model for the assessment of changes in habitat quality under different scenarios that may
134 occur with future development of the region or under management actions that could be
135 adopted to fulfill environmental conservation policies.

136

137 **2. Methods**

138 **Case study site**

139 The Llobregat River basin is an example of highly populated, severely exploited and
140 impacted area in the Mediterranean region. The basin has 4950 km² and the Llobregat
141 River, which flows from the Pyrenees Mountains to the Mediterranean Sea, is one of
142 the main water sources for the city of Barcelona and its metropolitan area, with a
143 population of 3 million people. Population and industry mainly concentrate in the lower
144 basin, whereas forest and grassland are more predominant in the upper part of the
145 basin (Fig. 1a). The basin is affected by many disturbances, ranging from diffuse
146 agricultural pollution to obstacles to connectivity such as dams or weirs, or important
147 water abstractions for industrial and domestic purposes, among others (Fig.1b-j).

148 **Description of the habitat quality model**

149 We apply the habitat quality module of InVEST (v.2.4.4; Kareiva et al., 2011; Tallis et al.,
150 2011), which combines information on LU/LC suitability and threats to biodiversity to
151 produce habitat quality maps. This approach generates information on the relative extent
152 and degradation of different habitat types in a region which can be useful for making an
153 initial assessment of conservation needs and for projecting changes across time. The
154 model is based on the hypothesis that areas with higher quality habitat support higher
155 richness of native species, and that decreases in habitat extent and quality lead to a decline
156 in species persistence.

157 Habitat quality in the InVEST model is estimated as a function of: (1) the suitability of each
158 LU/LC type for providing habitat for biodiversity, (2) the different anthropogenic threats likely
159 impairing habitat quality, and (3) the sensitivity of each LU/LC type to each threat. A LU/LC
160 map from the study area based on data from Landsat-TM was obtained from the Catalan
161 Government for year 2002, and land uses were aggregated in 10 different categories

162 corresponding to habitat types (Fig. 1a). A relative habitat suitability score H_j from 0 to 1,
163 where 1 indicates the highest suitability for species, was assigned to each habitat type.
164 Forest was the terrestrial habitat type with the highest habitat suitability for native species,
165 since it was considered the less modified habitat, while aquatic habitat suitability increased
166 with increasing stream size (related to the stream order). A significant characteristic of the
167 InVEST model is its ability to characterize the sensitivity of habitat types to various threats.
168 Not all habitats are affected by all threats in the same way, and the model accounts for this
169 variability. The source of each threat is mapped on a raster in which the value of the grid
170 cell, normalized between 0 and 1, indicates the intensity of the threat within the cell (Table
171 1). The impacts of threats on the habitat in a grid cell are mediated by three factors: (1) the
172 distance between the cell and the threat's source (to account for that, a maximum distance
173 over which the threat affects habitat quality is defined, $Max.D$); (2) the relative weight of
174 each threat (W_r , importance of one threat compared to the others); and (3) the relative
175 sensitivity of each habitat type to the threat (S_{jr}). In general, the impact of a threat on habitat
176 decreases as distance from the degradation source increases, so that cells closer to threats
177 will experience higher impacts and those further away than the $Max.D$ will not be impacted
178 by the threat at all. As some threats may be more damaging to habitat than others, W_r
179 indicates the relative destructiveness (0-1) of a degradation source to all habitats. The
180 model also assumes that the more sensitive a habitat type is to a threat (higher S_{jr}), the
181 more degraded the habitat type will be by the threat. In our study, H_j and the threat
182 parameters were initially determined from expert knowledge (Kuhnert et al., 2010) (see raw
183 survey data in the Supplementary Information). Ten experts with different ecological
184 backgrounds, ranging from experimental ecology to ecological modeling, were asked to
185 propose values for the model parameters for the case study. Prior to expert scoring, the
186 functioning of the habitat quality model, the parameters that experts were asked to provide
187 values for, and the structure and meaning of the tables they should fill in, were described in
188 detail. Experts were allowed to ask questions and discuss aspects that were not well
189 understood to ensure that their responses addressed the questions adequately. No result

190 sharing or feedback was allowed amongst the group during the elicitation process, meaning
 191 that our method relies on the experts having a good understanding of the questions being
 192 asked. However, in the case of identifying inconsistencies in the experts' responses, the
 193 values were excluded from the calculation. Mean and standard deviation values obtained
 194 from expert knowledge were used to calculate the model uncertainty. The sum of the total
 195 threat's level in a grid cell x of habitat type j provided a degradation score D_{xj} for the cell
 196 (equation 1) that was then used along with habitat suitability to compute a score of habitat
 197 quality Q_{xj} (equation 2). z and k in Eq. 2 are scaling parameters. Values finally used as input
 198 parameters for the habitat quality model are reported in Tables 1 and 2. These values were
 199 adjusted using the data elicited from expert knowledge as departure information, and
 200 subsequently contrasting the results with the assessment of the general status (ecological
 201 and chemical status) of water bodies obtained by the regional water authority (ACA, 2013).
 202 Adjustments applied to initial values obtained through expert knowledge consisted in
 203 increasing by 20% the value of S_{jr} for aquatic habitats, and the values of W_r and $Max.D$ for
 204 all threats. W_r and $Max.D$ values used for terrestrial threats fall within the range of values
 205 applied elsewhere (Polasky et al. 2011), but no values could be found for aquatic threats.
 206 The values obtained for habitat quality after model application range from 0 to 1, with 1
 207 meaning the highest habitat quality (see InVEST user's guide for further detail on this
 208 method).

$$209 \quad D_{xj} = \sum_{r=1}^R \sum_{y=1}^Y \left(\frac{W_r}{\sum_{r=1}^R W_r} \right) r_{y \text{ rxy}} i_{jr} S_{jr} \quad (1)$$

$$210 \quad Q_{xj} = H_j \left(1 - \left(\frac{D_{xj}^z}{D_{xj}^z + k^z} \right) \right) \quad (2)$$

211 We modified the habitat quality module of InVEST in order to simultaneously assess habitat
212 quality in both terrestrial and aquatic ecosystems. The modification consists in the
213 consideration of the river directional component when modeling the impact of aquatic
214 threats. Also, whereas terrestrial threats are considered to impact all types of habitat, we
215 assume that aquatic threats only affect aquatic habitat types. Both types of threats are
216 modeled as decaying exponentially, but whereas terrestrial threats extend in all directions
217 of the landscape, aquatic threats only impact areas downstream of the threat source. A flow
218 direction map is used to select as impacted only the aquatic cells (stream cells) located
219 downstream from the threat source and within the maximum distance of affectation. This is
220 important not just because these threats affect only the aquatic ecosystems, but also
221 because the distance of the threats' effects is not straight but follows the flow path
222 downstream.

223 **Validation of the habitat quality model**

224 We estimated habitat quality in terrestrial and aquatic ecosystems, and compared those
225 estimates with existing values of terrestrial and aquatic biodiversity within the basin to
226 assess the model reliability. The results obtained with the habitat quality model needed to
227 be validated because many parameters were defined through expert knowledge and
228 biodiversity occurrence or distribution data were not used to build the model. Data on
229 vascular plant richness collected from orthophotos and field work for the period 1996-2006
230 (Barcelona's Council, 2009) was therefore compared to the modeled terrestrial habitat
231 quality, and data on macroinvertebrate diversity collected during periodic samplings (for
232 years 2010-11) of the regional water agency (ACA) were compared to aquatic habitat
233 quality. For the calculation of aquatic macroinvertebrate diversity only the abundance of
234 taxa normally found in clean water was considered. In addition, we used data on the
235 average annual in-stream phosphorous retention in the Llobregat river (Aguilera et al.,
236 2013) to explore the relationship between aquatic habitat quality and aquatic ecosystem
237 functioning. Data on in-stream phosphorus retention were calculated for the period 2000-06

238 applying SPARROW, a statistical mechanistic modeling tool. Phosphate concentrations
239 were obtained from locations monitored by the ACA.

240 In order to assess the response/sensitivity of the model to scenario change, we applied the
241 model to different development and management scenarios by means of quantifying the
242 percentage of change in the obtained habitat quality of the Llobregat basin under 3
243 hypothetical cases: (1) increase of 15% urban land use (expanding from the existing urban
244 areas by adding an adequate buffer around actual urban areas); (2) increase of 15%
245 forest cover in the entire basin (expanding from the main existing forest areas by adding an
246 adequate buffer around actual forest areas); and (3) removal of small dams or weirs
247 (obstructions smaller than most conventional dams) while keeping the main reservoirs in
248 place. Weirs in the Llobregat basin are a main concern for stream connectivity. In total,
249 more than 100 weirs exist in the basin, with three main big reservoirs located in the
250 northern part. While a threat layer containing the three main reservoirs together with all the
251 weirs was used for dams in the baseline scenario, a threat layer containing only the three
252 main reservoirs was used after the removal of small dams. Results obtained at the grid cell
253 level were subsequently aggregated at the sub-basin scale (by averaging cell values) for
254 interpretation purposes. Sub-basins were defined based on the Water Framework Directive
255 water bodies design and were further sub-divided into smaller sub-basins using the 200m
256 cell-size DEM to identify tributary junctions.

257

258 **3. Results**

259 **3.1. Modeled current habitat quality in the Llobregat basin**

260 There was high spatial heterogeneity in modeled habitat quality in the Llobregat basin (Fig.
261 2a). Forested areas in the northern and central parts of the basin (blue areas) had a higher
262 habitat quality than areas closer to the river mouth (red areas), where the major urban
263 settlements occur. Mean aquatic habitat quality in the basin was 25% lower than mean
264 terrestrial habitat quality

265 The average uncertainty for the determination of habitat quality in the Llobregat basin was
266 23%, based on the coefficient of variation of the mean scores obtained by expert judgment
267 across the whole basin. The uncertainty of habitat quality scores was higher for aquatic
268 (34%) than for terrestrial ecosystems (23%). Urban areas and reservoirs were the habitat
269 types with the highest uncertainty in the estimation of habitat quality (82% and 73%
270 respectively), while habitat types with lower uncertainty prediction were non-irrigated
271 agriculture and forest (14% and 19% respectively).

272 **3.2. Habitat quality as a proxy for biodiversity**

273 The model provided fairly accurate proxies for certain aspects of biodiversity. Modeled
274 terrestrial habitat quality explained 76% of the variation in the observed index of vascular
275 plant richness ($p < 0.0001$, Fig. 3a). Modeled aquatic habitat quality explained 34% of the
276 variation in the observed diversity of the macroinvertebrate community ($p < 0.0001$, Fig.
277 3b). Habitat quality also explained 45% of the variation in in-stream phosphate retention (p
278 < 0.0001 , Fig. 3c).

279 **3.3. Model application to scenario analysis**

280 The model proved to be sensitive to all analyzed scenarios, especially for aquatic habitat
281 quality, which was always more impacted than terrestrial habitat quality (Fig. 2). A scenario
282 of 15% urban expansion (involving an increase of around 4450 ha of urban cover) caused a

283 decrease in the mean habitat quality of the basin. Mean decreases in aquatic and terrestrial
284 habitat quality were 2% and 0.8% respectively (Fig. 2 b-c). Sub-basin habitat quality
285 decreases of more than 25% were confined to the south-east portion of the basin for both
286 terrestrial and aquatic ecosystems. The scenario of 15% increase in forest land cover
287 (involving an increase of around 28200 ha of forest) caused the highest change in the
288 average habitat quality of the basin. Mean improvements of aquatic and terrestrial habitat
289 quality were 9.7% and 1.9% respectively (Fig. 2 d-e). At the sub-basin scale, forest
290 expansion increased the current habitat quality of aquatic ecosystems by more than 50% in
291 some northern sub-basins. However, when looking at results per hectare, urban expansion
292 generated a higher impact than forest expansion on both terrestrial and aquatic habitat
293 quality. The average increase in aquatic habitat quality following small dams' removal was
294 2.2%, (Fig. 2f). Dam removal at the sub-basin scale had the highest impact in the middle
295 part of the basin, in the Llobregat river mainstem, where 5 - 25 % increases in aquatic
296 habitat quality were predicted.

297 **4. Discussion**

298 The modified habitat quality module of InVEST proved useful as a surrogate for biodiversity
299 for terrestrial and aquatic ecosystems. With relatively low data requirements (only
300 information on LU/LC and threats), the model provides a spatially explicit representation of
301 habitat quality that correlates with biodiversity at the river basin scale. The combination of
302 terrestrial and aquatic threats is particularly important for the environmental management of
303 river basins, since traditionally the aquatic compartment has received less attention despite
304 being affected by the interaction of both types of threats.

305 The correlation between observed indicators of biodiversity and modeled habitat quality in
306 the study basin indicates an accurate direction of the response of biodiversity. However, we
307 should take into account that no single biological indicator provides all the information
308 needed to interpret the response of an entire ecosystem. A good fit was obtained for the
309 terrestrial biodiversity indicator, which agrees with the relationship between habitat
310 degradation and vascular plants identified elsewhere (Evans et al., 2011). The lower
311 goodness-of-fit obtained for the aquatic biodiversity indicator (Fig.3b) probably reflects the
312 relevance of stream temporal dynamics, which is not considered in the model but plays a
313 large role in determining the aquatic species at the moment of sampling. It may also be due
314 to the selection of a single community (macroinvertebrates), which provides a limited
315 representation of aquatic biodiversity. The number of samples and spatial coverage of
316 macroinvertebrate data was lower than that for plant richness, and this also likely
317 contributed to the lower goodness-of-fit between modeled habitat quality and observed
318 aquatic biodiversity. Additionally, expert knowledge associated the highest aquatic habitat
319 suitability to the highest-size stream reaches. This agrees with the work of Statzner and
320 Higler (1985), who found that a higher plankton development in the lower stream reaches
321 made the number of fish species increase, therefore influencing the diversity patterns of the
322 whole community. This assumption does not entirely follow the River Continuum Concept
323 that describes a maximization of biotic diversity in mid-reaches of streams as a result of the

324 occurrence of highest environmental variability (Vannote et al., 1980). On the other hand,
325 studies exist that found no relationship between biodiversity and stream order (Statzner,
326 1981) or that diversity is almost constant throughout different orders (Minshall et al., 1982).
327 The observed trend will probably depend on the particular characteristics of the study area,
328 thus the assumption of either one hypothesis or another can affect the obtained results. In-
329 stream nutrient retention was significantly correlated with the estimated aquatic habitat
330 quality, indicating that the more degraded the habitats, the lower the species diversity and
331 the lower the ecosystem functioning. Although we cannot infer a mechanism based solely
332 on this correlation, it is consistent with the theory that biodiversity affects the functioning of
333 ecosystems, with implications for the services that we obtain from ecosystems, such as
334 water purification (Loreau et al., 2001; Hooper et al., 2005; Balvanera et al., 2006;
335 Cardinale et al., 2012).

336 Habitat degradation in the Llobregat basin, as well as in many other multiple-use basins,
337 was more pronounced near urban settlements and in the lower watercourses because of
338 the accumulation of threats coming from upstream. This supports previous findings
339 identifying urban LU/LC as a major threat to natural ecosystems (Martinuzzi et al., 2014),
340 and demonstrating the compounding of threats in the downstream direction along major
341 river corridors (Vörösmarty et al., 2010). Urban settlements together with agriculture,
342 livestock grazing, infrastructure, and extractive activities were identified as the threats
343 causing the highest habitat loss for terrestrial and freshwater species in Australia (Evans et
344 al., 2011). A similar analysis developed in the marine realm (Halpern et al. 2008) identified
345 that no area was unaffected by human influence and that a large fraction of the global
346 landscape (41%) was strongly affected by multiple drivers. Only large areas of relatively
347 little human impact were identified in the poles, where human access is limited. Unlike our
348 approach, that uses threats to obtain habitat quality (as a surrogate of species distribution),
349 the approach followed by Evans et al., (2011) was based on species distribution as a
350 surrogate for threats. In agreement with our results, they also found that freshwater species

351 were more affected by threats than terrestrial species. The higher habitat degradation in
352 aquatic ecosystems is certainly partly due to the reduction in habitat suitability values, but
353 may be also an artifact of the approach followed, as aquatic habitat quality was affected by
354 a higher number of threats than terrestrial habitat quality, coming from both land and water.
355 In this work we assume aquatic threats to propagate only in the downstream direction.
356 However, while this can work for the major part of considered threats, it overlooks the
357 upstream impact of barriers such as weirs and dams that can also constrain the upstream
358 movement of aquatic species. Although some parameter values used in the model (Tables
359 1 and 2) are case-specific, others can be transferred to other Mediterranean basins with
360 similar characteristics when site-specific data are not available. This is the case of the
361 habitat sensitivity to threats, S_{jr} , and the maximum distance of threat affectation, $Max.D$. On
362 the other hand, the threat weight, W_r , depends on the importance of threats within the study
363 area, which will be different in each basin. Only when general biodiversity is considered,
364 can the values for habitat suitability, H_j , be transferred. Otherwise, specific values for the
365 considered species need to be defined.

366 Although in the scenario analysis exercise the 15 % forest expansion produced the highest
367 variation in habitat quality when compared to the same percentage of urban expansion, this
368 increase was due to the fact that the area of forest was approximately 6 times higher than
369 the urban area. Results per hectare showed a higher impact of urban expansion on habitat
370 quality, even though all results should be interpreted while taking into account the model
371 uncertainty. A caveat to the apparent increase in biodiversity resulting from forest
372 expansion is that replacing other natural vegetation types with forest could lower
373 landscape-level biodiversity by homogenizing the landscape and eliminating distinct sets of
374 species not found in forests. This level of diversity (β diversity) is not considered in the
375 current approach, since the aim of this work is to assess the sensitivity of the model
376 presented. The increase in habitat quality after dam's removal was possibly underestimated

377 because, as already stated, the upstream impact of these obstacles was not accounted in
378 the modeling.

379 The model responsiveness to the selected scenarios of LU/LC and threat change confirms
380 its suitability for scenario analysis. The modified module of habitat quality of InVEST is
381 comparable to other approaches that are commonly used in conservation planning amidst
382 myriad threats to the environment, like GLOBIO (UNEP, 2001; Alkemade et al., 2009) or
383 the International Union for Conservation of Nature approach (IUCN, 2007). The simple yet
384 robust InVEST approach could complement other spatial prioritization and systematic
385 conservation planning tools that have been applied to both terrestrial and aquatic
386 ecosystems, such as C-Plan, ConsNet, Marxan, Resnet or Zonation (reviewed in Moilanen
387 et al., 2009). Although the utility of estimates of species richness as metrics for
388 conservation planning has limitations (Fleishman et al., 2006), these metrics can contribute
389 to prioritizing locations for biodiversity conservation when used together with additional
390 metrics such as species composition, endemism, functional significance, and severity of
391 threats. The strength of this modified InVEST model is that it can provide reliable
392 indications of the biodiversity response to future threats for both terrestrial and aquatic
393 ecosystems, without requiring any prior information about species distribution or
394 presence/absence data (other than data to be used for calibration). This makes the model
395 especially useful in areas where such data is poor, although caution is needed in using the
396 results without proper validation. The modified InVEST habitat quality model may be used
397 to assess how human activities can be spatially managed to reduce their negative impacts
398 on ecosystems. Whether to inform prioritization and systematic conservation tools or
399 related conservation planning decisions, it can help assess current habitat quality and
400 provide information on habitat quality and biodiversity changes caused by different
401 conservation actions.

402

403 **5. Conclusions**

404 We have improved the existing habitat quality module of the InVEST suite of models by
405 including the ability to additionally assess aquatic habitat quality. The relatively good
406 goodness-of-fit between modeled habitat quality and terrestrial and aquatic biodiversity
407 indicators in a case study river basin affected by multiple threats demonstrated the reliability
408 of the model. By evaluating scenarios of change in LU/LC and threats to biodiversity, we
409 provide an example of the potential use of the model for supporting decision making in land
410 and water management planning. Therefore, we believe that because of its simplicity and
411 the use of readily available data, the developed model can help decision-makers in the
412 trade-off analysis of management actions in river basins worldwide.

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Tables

Table 1. Characteristics of threats to habitat quality considered in the Llobregat river basin.

Threats	Representation (intensity)	Direction of propagation	W_r^* [0-1]	Max.D* (km)
Terrestrial				
Urbanization	Urbanization density (high 1, low 0.5)	All	1.00	7.1
Agriculture	Irrigation (1) vs non-irrigation (0.5)	All	0.68	4.0
Roads	Road network (1)	All	0.71	2.9
Mining	Active (1) vs inactive mines (0.5)	All	0.80	5.6
Aquatic				
Dams	Big reservoirs (1) vs smaller dams (0.5)	Downstream	0.92	14.0
WWTPs	Organic load: dissolved organic carbon x flow (normalized [0-1])	Downstream	0.83	6.0
Water abstraction	Annual extracted water volume (normalized [0-1])	Downstream	0.77	13.2
Channeling	Channelized reaches (1)	None	0.76	0.0
Invasive species	Number of identified invasive species (normalized [0-1])	None	0.68	0.0

* W_r and Max.D refer to the mean values of weights and maximum distance over which the threats affect habitat quality, and were obtained based on data elicited from expert knowledge and subsequently adjusted during the calibration of the habitat quality model using empirical biodiversity data.

Table 2. Mean values for habitat suitability (H_j) and the relative sensitivity of habitat types to threats (S_{jr}) considered in the Llobregat river basin, obtained based on data elicited from expert knowledge and subsequently adjusted during the calibration of the habitat quality model using empirical biodiversity data.

Habitat type	H_j [0-1]	Relative sensitivity of habitat types to threats (S_{jr})								
		Urbanization	Agriculture	Roads	Mining	Dams	WWTPs	Water abstraction	Channeling	Invasive species
Urban	0.15	0.01	0.16	0.10	0.19	-	-	-	-	-
Ag.Non-irrigated	0.55	0.72	0.01	0.58	0.63	-	-	-	-	-
Ag.Irrigated	0.40	0.69	0.03	0.59	0.65	-	-	-	-	-
Grass/shrubland	0.72	0.75	0.67	0.70	0.68	-	-	-	-	-
Forest	0.93	0.85	0.70	0.78	0.72	-	-	-	-	-
Reservoirs	0.33	0.42	0.60	0.29	0.60	0.06	0.72	0.60	0.12	0.79
Stream size 1	0.65	1.00	0.92	0.86	0.96	1.00	1.00	1.00	1.00	0.88
Stream size 2	0.70	1.00	0.84	0.78	0.89	1.00	0.97	0.96	0.94	0.82
Stream size 3	0.75	0.96	0.79	0.68	0.80	0.90	0.86	0.84	0.85	0.76
Stream size 4	0.80	0.91	0.71	0.65	0.74	0.80	0.76	0.73	0.77	0.70

Figures

Figure 1. Maps of habitat types (a) and location and magnitude of the terrestrial (b-e) and aquatic (f-j) threats in the Llobregat river basin. Considered threats: (b) urbanization; (c) agriculture; (d) roads; (e) mines; (f) dams; (g) wastewater treatment plants; (h) water abstractions; (i) channeling; (j) invasive species.

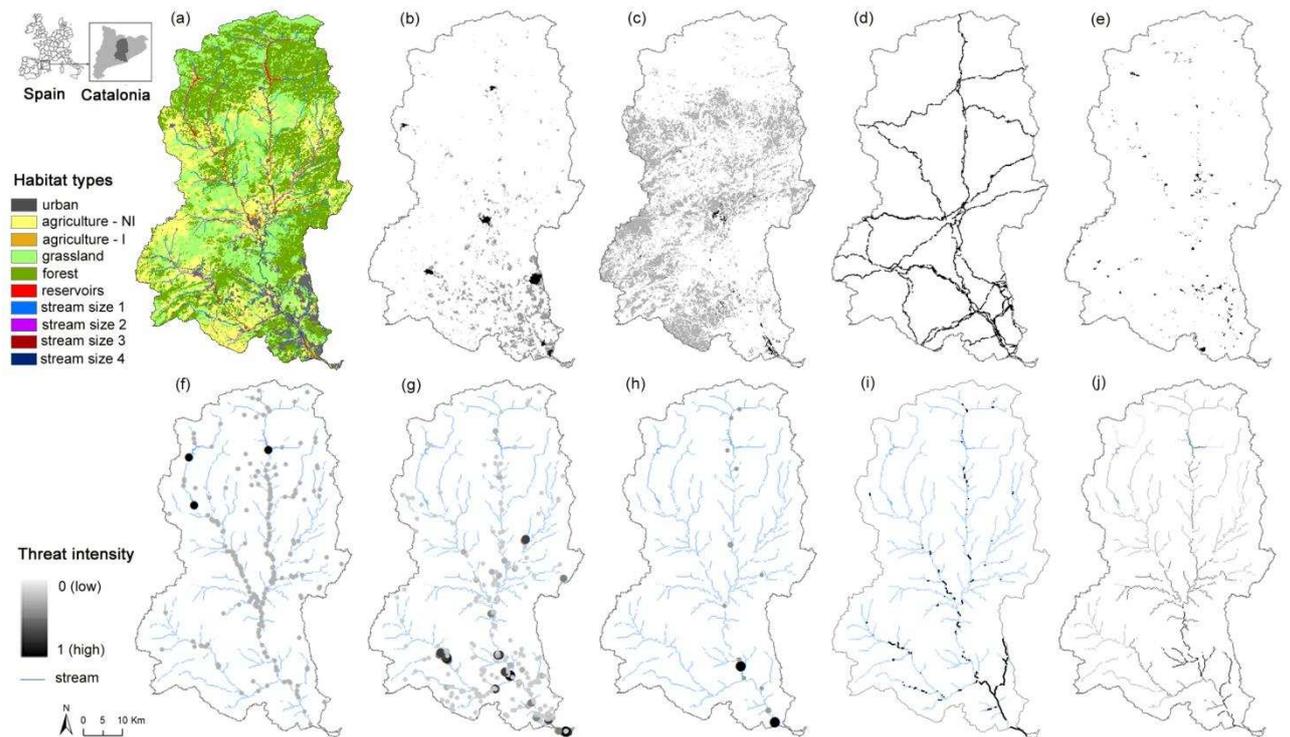


Figure 2. Current habitat quality in the Llobregat river basin (a) and change in terrestrial and aquatic habitat quality at the sub-basin scale under different scenarios: increase of 15% urban land cover (b-c), increase of 15% forest land cover (d-e), and removal of small dams (only for aquatic) (f). Habitat quality scores differentiate areas according to their higher or lower habitat quality and, therefore, to their higher or lower capacity to host biodiversity. Number below each map corresponds to the percentage change in habitat quality. In brackets, maximal change per sub-basin.

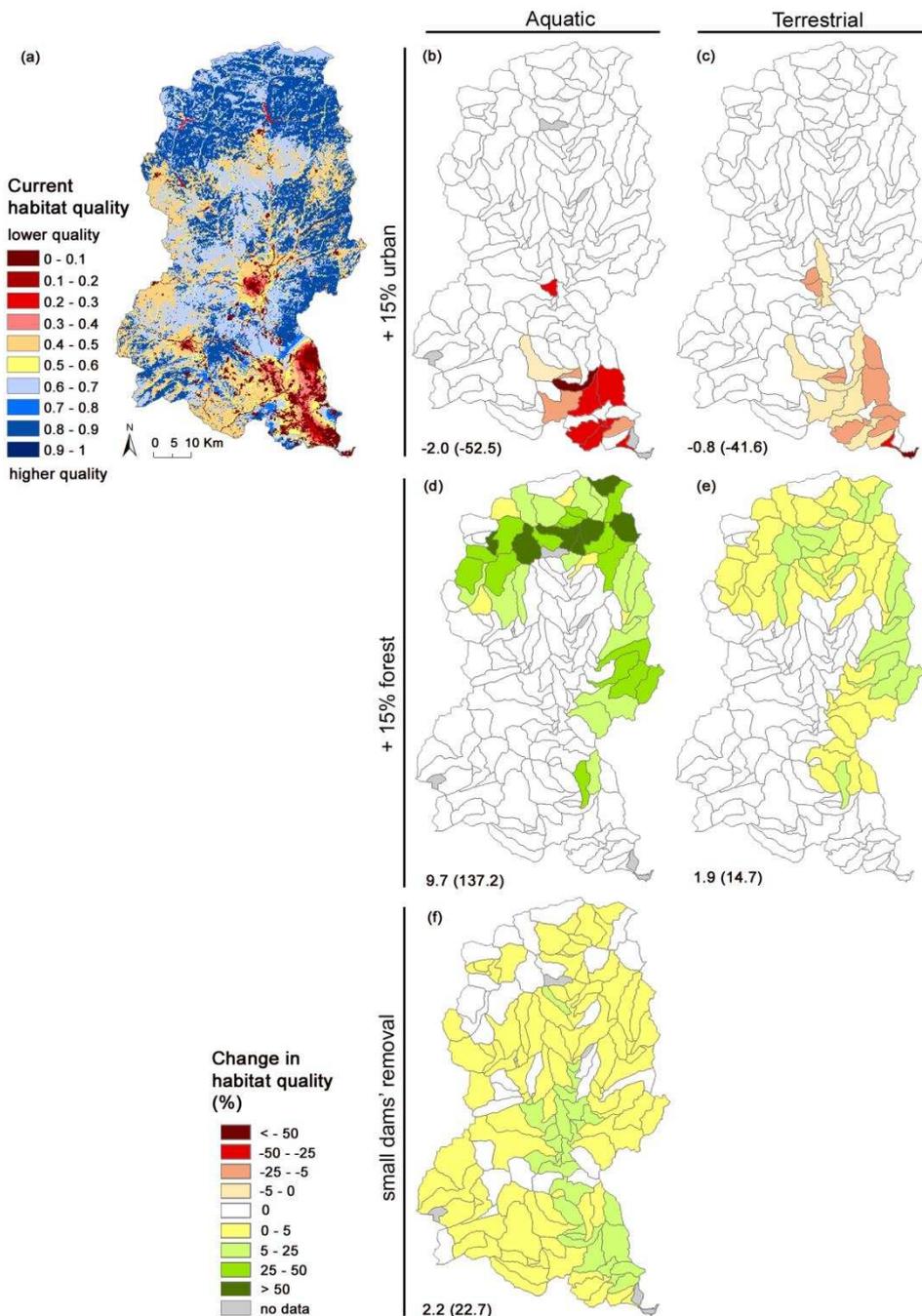


Figure 3. Relationship between modeled habitat quality and observed indicators of biodiversity and ecosystem functioning in the Llobregat River basin: terrestrial habitat quality versus plant richness (a); aquatic habitat quality versus macroinvertebrate Shannon diversity (H') (b); aquatic habitat quality versus ecosystem functioning (mean in-stream phosphate removal) (c).

