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

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HIGHLIGHTS

- We present a model for the simultaneous assessment of land & aquatic habitat quality.
- We assess the reliability of the model as a proxy for biodiversity in river basins.
- We demonstrate the suitability of the model for scenario analysis in river basins.
- We recommend the model to assess biodiversity changes of conservation planning actions.

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ABSTRACT

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

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1. Introduction

Loss and degradation of natural habitats is a primary cause of declining biodiversity (Fuller et al., 2007), yet humans must balance conservation with development needs. It is difficult to strike such a balance with inadequate information about the consequences of our land use and management decisions. Nevertheless, we do know that the main drivers of the decrease in habitat quality are land use and climate change (Sala et al., 2000), which are exacerbated by other anthropogenic threats such

as the construction of infrastructure and the introduction of exotic species (Ricciardi and Rasmussen, 1999). Worldwide, species extinction in freshwater environments is estimated to be higher than in terrestrial ecosystems (McAllister et al., 1997; Abell, 2002). Despite their reduced extent, freshwater systems support 10% of all known species (Carrizo et al., 2013). One of the reasons for higher extinction rates in freshwater is the difficulty of conservation efforts. Freshwater systems are susceptible not only to direct impacts but also to indirect impacts from disturbances elsewhere in the basin, all of which can contribute to the loss of biodiversity in rivers. Whereas many terrestrial conservation programs consider only threats adjacent to the site of interest, conservation of freshwater systems needs to take into account the connected nature of rivers, which present a strong directional component (Ward et al., 2002; Moilanen et al., 2008; Linke et al., 2011).

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Maintaining and protecting habitat quality and biodiversity, while still meeting human needs, is an urgent task in ecosystems management. Efforts to preserve biodiversity have resulted in the creation of a variety of environmental policies, like the ambitious new strategy adopted in 2012 by the European Parliament to halt the loss of biodiversity and ecosystem services in the European Union (EU) by year 2020, or the USA Endangered Species Act of 1973, and the Fish and Wildlife Conservation Act of 1980 (Goble et al., 2005; Stoms et al., 2010; EC, 2011). Other laws are oriented to restoring and maintaining the biological integrity of freshwater ecosystems, such as the Water Framework Directive of year 2000 in the EU, or the Clean Water Act of 1965 in the USA (Karr, 1991; Griffiths, 2002). Major conservation efforts also exist in emerging economies such as China, which committed to setting aside 23% of the country as priority conservation areas through the Strategy and Action Plan for Biodiversity Conservation of 2010 (MEPC, 2011). Similarly, some Latin American countries have progressive conservation policies, like Costa Rica's Biodiversity Law of 1998 and Colombia's National System of Protected Areas of 2010 (Solís-Rivera and Madrigal-Cordero, 1999; Vasquez and Serrano, 2009).

Environmental policies should go along with further understanding of the necessary actions to preserve habitats and species (Strayer and Dudgeon, 2010). Scenario analysis has proved useful for assessing the effects of specific management actions on biodiversity (Kass et al., 2011; Nelson et al., 2011; Carwardine et al., 2012), identifying vulnerability to global change (Pereira et al., 2010; Domisch et al., 2013), and guiding conservation planning (Dauwalter and Rahel, 2008; Hermoso et al., 2011; Moilanen et al., 2011). Thus, central to any conservation strategy throughout the world has been the establishment of protected areas, which has led to the evolvement of systematic conservation planning. Regarding this, systematic conservation tools have been designed to help planners decide on the location and configuration of conservation areas, so that the biodiversity value of each area can be maximized. Among these tools we find models like Marxan (Ball et al., 2009), Zonation (Moilanen et al., 2009), C-Plan (Pressey et al., 2009) or ConsNet (Sarkar et al., 2006). Recent conservation efforts have also used species distribution models to deliver insights into the relationship between biodiversity and the environment (Elith and Leathwick, 2009; Vander Laan et al., 2013; Kuemmerlen et al., 2014). These models usually relate known occurrences of a species with environmental conditions and predict occurrences in areas where suitable environmental conditions are known but no occurrence data are available. More recently, focus has shifted towards understanding and incorporating the distribution of threats (Allan et al., 2013; Tulloch et al., 2015). Approaches to threat mapping range from mapping the distribution of a single threat to additive scoring approaches for multiple threats that incorporate ecosystem vulnerability (Evans et al., 2011; Coll et al., 2012; Auerbach et al., 2014). Models that predict the status of biodiversity as a function of anthropogenic threats using biodiversity proxies are useful to inform management. Such models include GLOBIO (Alkemade et al., 2009) and InVEST (*Integrated Valuation of Environmental Services and Tradeoffs*; Tallis et al., 2011; Sharp et al., 2014), that are based on the mean species abundance (MSA) and on estimates of habitat quality respectively. However, proxy effectiveness as an adequate indicator of biodiversity has not been fully tested (Eigenbrod et al., 2010), and this can only be achieved by rigorous comparison of biodiversity proxies such as habitat quality to different indicators of biodiversity (either species richness, taxa, rarity, etc.) over space and time. Unlike GLOBIO, that uses a biodiversity index related to a baseline corresponding to the similarity to the natural situation, InVEST requires assessing which habitat type reflects natural conditions the best. The InVEST habitat quality model has successfully been applied to estimate the impact of different scenarios of land use/land cover (LU/LC) change or conservation policies on terrestrial habitat for biodiversity (Polasky et al., 2011; Bai et al., 2011; Nelson et al., 2011; Leh et al., 2013; Baral et al., 2014). Since InVEST is by now exclusively estimating the habitat quality of terrestrial ecosystems, developing tools that include the aquatic compartment together

with the terrestrial is highly advisable given the increasing concern for freshwater biota and the interrelation of the two compartments. Both terrestrial and aquatic components play an important role in environmental management for habitat protection (Palmer et al., 2008).

In this study, we adapt the deterministic spatially-explicit habitat quality module of the InVEST suite of models for the assessment of habitat quality in river basins, considering the effects of anthropogenic threats on terrestrial and aquatic habitat. The extension of the module to assess aquatic ecosystems is one of the improvements presented in this work. Our goal is to provide a simple model that can be used to reliably assess the effects of ongoing threats and environmental management actions on habitat quality and current levels of biodiversity, and that allows for scenario analysis in order to forecast the effects of future management actions. We select the InVEST model because it proceeds with data on LU/LC, anthropogenic threats and expert knowledge, to obtain reliable indicators about the current and future response of biodiversity to threats, and because unlike other approaches used in biodiversity conservation, it does not require prior information about the distribution or presence of species. To illustrate the performance of the model, we apply it to the case study of a severely impaired basin in the Mediterranean region (Llobregat River basin, NE Iberian Peninsula). We test the reliability of the model by comparing the estimated habitat quality values with observed terrestrial and aquatic biodiversity data. We also check the response of the model for the assessment of changes in habitat quality under different scenarios that may occur with the future development of the region or under management actions that could be adopted to fulfill environmental conservation policies.

2. Methods

2.1. Case study site

The Llobregat River basin is an example of a highly populated and severely exploited and impacted area in the Mediterranean region. The basin has 4950 km^2 and the Llobregat River, which flows from the Pyrenees Mountains to the Mediterranean Sea, is one of the main water sources for the city of Barcelona and its metropolitan area, with a population of 3 million people. Population and industry mainly concentrate in the lower basin, whereas forest and grassland are more predominant in the upper part of the basin (Fig. 1a). The basin is affected by many disturbances, ranging from diffuse agricultural pollution to obstacles to connectivity such as dams or weirs, or important water abstractions for industrial and domestic purposes, among others (Fig. 1b–j).

2.2. Description of the habitat quality model

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

Habitat quality in the InVEST model is estimated as a function of: (1) the suitability of each LU/LC type for providing habitat for biodiversity, (2) the different anthropogenic threats likely impairing habitat quality, and (3) the sensitivity of each LU/LC type to each threat. A LU/LC map from the study area based on data from Landsat-TM was obtained from the Catalan Government for year 2002, and land uses were aggregated in 10 different categories corresponding to habitat types (Fig. 1a). A relative habitat suitability score H_j from 0 to 1, where 1 indicates the highest suitability for species, was assigned to each habitat
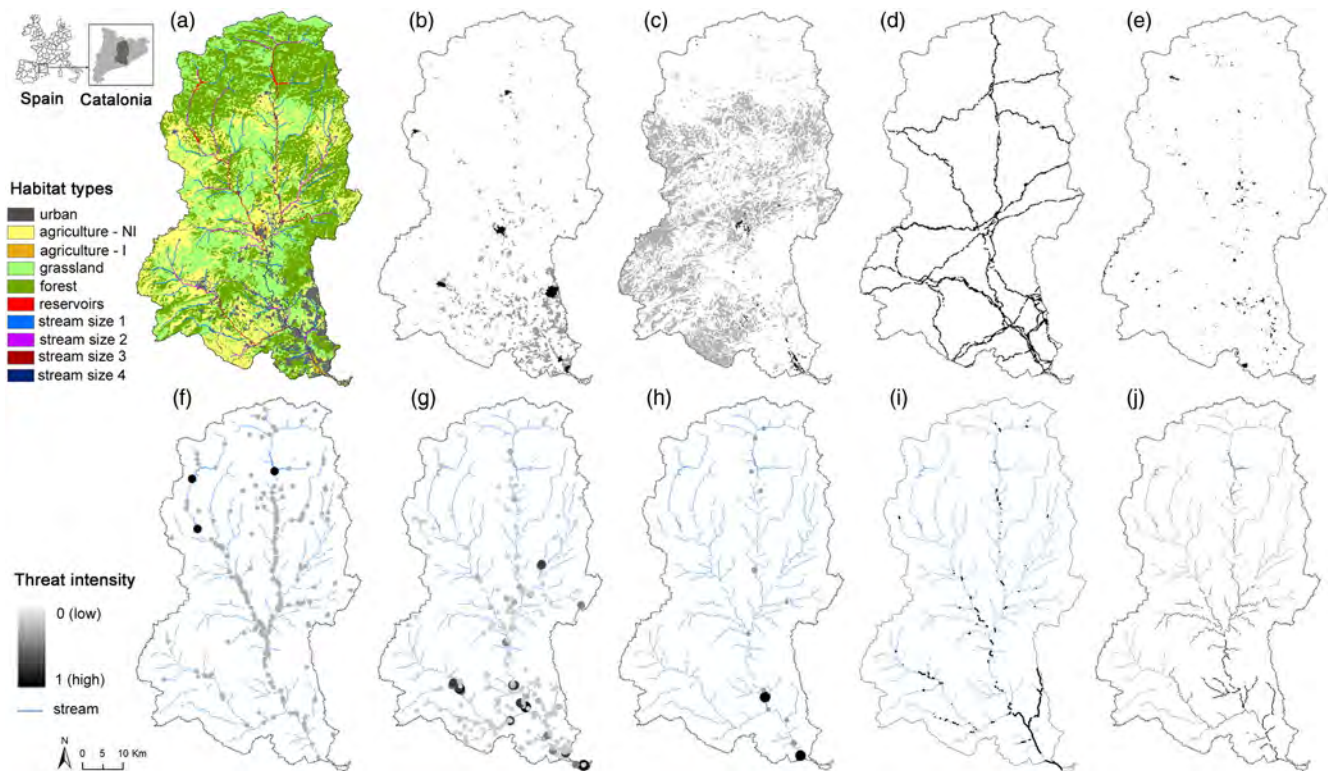
Fig. 1. Maps of habitat types (a) and location and magnitude of the terrestrial (b–e) and aquatic (f–j) threats in the Llobregat River basin. Considered threats: (b) urbanization; (c) agriculture; (d) roads; (e) mines; (f) dams; (g) wastewater treatment plants; (h) water abstractions; (i) channeling; (j) invasive species.

type. Forest was the terrestrial habitat type with the highest habitat suitability for native species, since it was considered the less modified habitat, while aquatic habitat suitability increased with increasing stream size (related to the stream order). A significant characteristic of the InVEST model is its ability to characterize the sensitivity of habitat types to various threats. Not all habitats are affected by all threats in the same way, and the model accounts for this variability. The source of each threat is mapped on a raster in which the value of the grid cell, normalized between 0 and 1, indicates the intensity of the threat within the cell (Table 1). The impacts of threats on the habitat in a grid cell are mediated by three factors: (1) the distance between the cell and the threat's source (to account for that, a maximum distance over which the threat affects habitat quality is defined, *Max.D*); (2) the relative weight of each threat (W_r, importance of one threat compared to the others); and (3) the relative sensitivity of each habitat type to the threat (S_{jr}). In general, the impact of a threat on habitat decreases as distance

from the degradation source increases, so that cells closer to threats will experience higher impacts and those further away than the *Max.D* will not be impacted by the threat at all. As some threats may be more damaging to habitat than others, W_r indicates the relative destructiveness (0–1) of a degradation source to all habitats. The model also assumes that the more sensitive a habitat type is to a threat (higher S_{jr}), the more degraded the habitat type will be by the threat. In our study, H_j and the threat parameters were initially determined from expert knowledge (Kuhnert et al., 2010) (see raw survey data in the Supplementary data). Ten experts with different ecological backgrounds, ranging from experimental ecology to ecological modeling, were asked to propose values for the model parameters for the case study. Prior to expert scoring, the functioning of the habitat quality model, the parameters that experts were asked to provide values for, and the structure and meaning of the tables they should fill in, were described in detail. Experts were allowed to ask questions and discuss aspects that were

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

Threats	Representation (intensity)	Direction of propagation	W_r [a] [0–1]	*Max.D* [a] (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 × 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

[a] 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 data from the ecological status of water bodies.

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 data from the ecological status of water bodies.

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	0.61	0.29	0.64	0.06	0.72	0.60	0.14	0.79
Stream size 1	0.66	1.00	0.94	0.88	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	0.76	0.96	0.79	0.70	0.82	0.90	0.86	0.84	0.85	0.76
Stream size 4	0.80	0.91	0.71	0.65	0.76	0.80	0.76	0.73	0.77	0.71

not well understood to ensure that their responses addressed the questions adequately. No result sharing or feedback was allowed among the group during the elicitation process, meaning that our method relies on the experts having a good understanding of the questions being asked. However, in the case of identifying inconsistencies in the experts' responses, the values were excluded from the calculation. Mean and standard deviation values obtained from expert knowledge were used to calculate the uncertainty of the model. The sum of the total threat's level in a grid cell x of habitat type j provided a degradation score D_{xj} for the cell (Eq. (1)) that was then used along with habitat suitability to compute a score of habitat quality Q_{xj} (Eq. (2)). z and k in Eq. (2) are scaling parameters. Values finally used as input parameters for the habitat quality model are reported in Tables 1 and 2. These values were adjusted using the data elicited from expert knowledge as departure information, and subsequently contrasting the results with the assessment of the ecological status of water bodies obtained by the regional water authority (ACA, 2013). Adjustments applied to initial values obtained through expert knowledge consisted in increasing by 20% the value of S_{rj} for aquatic habitats, and the values of W_r and Max.D for all threats. W_r and Max.D values used for terrestrial threats fall within the range of values applied elsewhere (Polasky et al. 2011), but no values could be found for aquatic threats. The values obtained for habitat quality after model application range from 0 to 1, with 1 meaning the highest habitat quality (see InVEST user's guide for further details on this method).

$$D_{xj} = \sum_{r=1}^{R} \sum_{y=1}^{Y_r} \left(\frac{w_r}{\sum_{r=1}^{R} w_r} \right) r_y i_{rxy} S_{jr}. \tag{1}$$

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

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

### 2.3. Validation of the habitat quality model

We estimated habitat quality in terrestrial and aquatic ecosystems, and compared those estimates with existing values of terrestrial and aquatic biodiversity within the basin to assess the reliability of the model. The results obtained with the habitat quality model needed to be validated because many parameters were defined through expert knowledge and biodiversity occurrence or distribution data were not used to build the model. Data on vascular plant richness collected from orthophotos and field work for the period 1996–2006 (Barcelona's Council, 2009) were therefore compared to the modeled terrestrial habitat quality, and data on macroinvertebrate diversity collected during periodic samplings (for years 2010–11) of the regional water agency (ACA) were compared to aquatic habitat quality. For the calculation of aquatic macroinvertebrate diversity only the abundance of taxa normally found in clean water was considered. In addition, we used data on the average annual in-stream phosphorous retention in the Llobregat River (Aguilera et al., 2013) to explore the relationship between aquatic habitat quality and aquatic ecosystem functioning. Data on in-stream phosphorus retention were calculated for the period 2000–06 applying SPARROW, a statistical mechanistic modeling tool. Phosphate concentrations were obtained from locations monitored by the ACA.

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

3. Results

3.1. Modeled current habitat quality in the Llobregat basin

There was high spatial heterogeneity in modeled habitat quality in the Llobregat basin (Fig. 2a). Forested areas in the northern and central
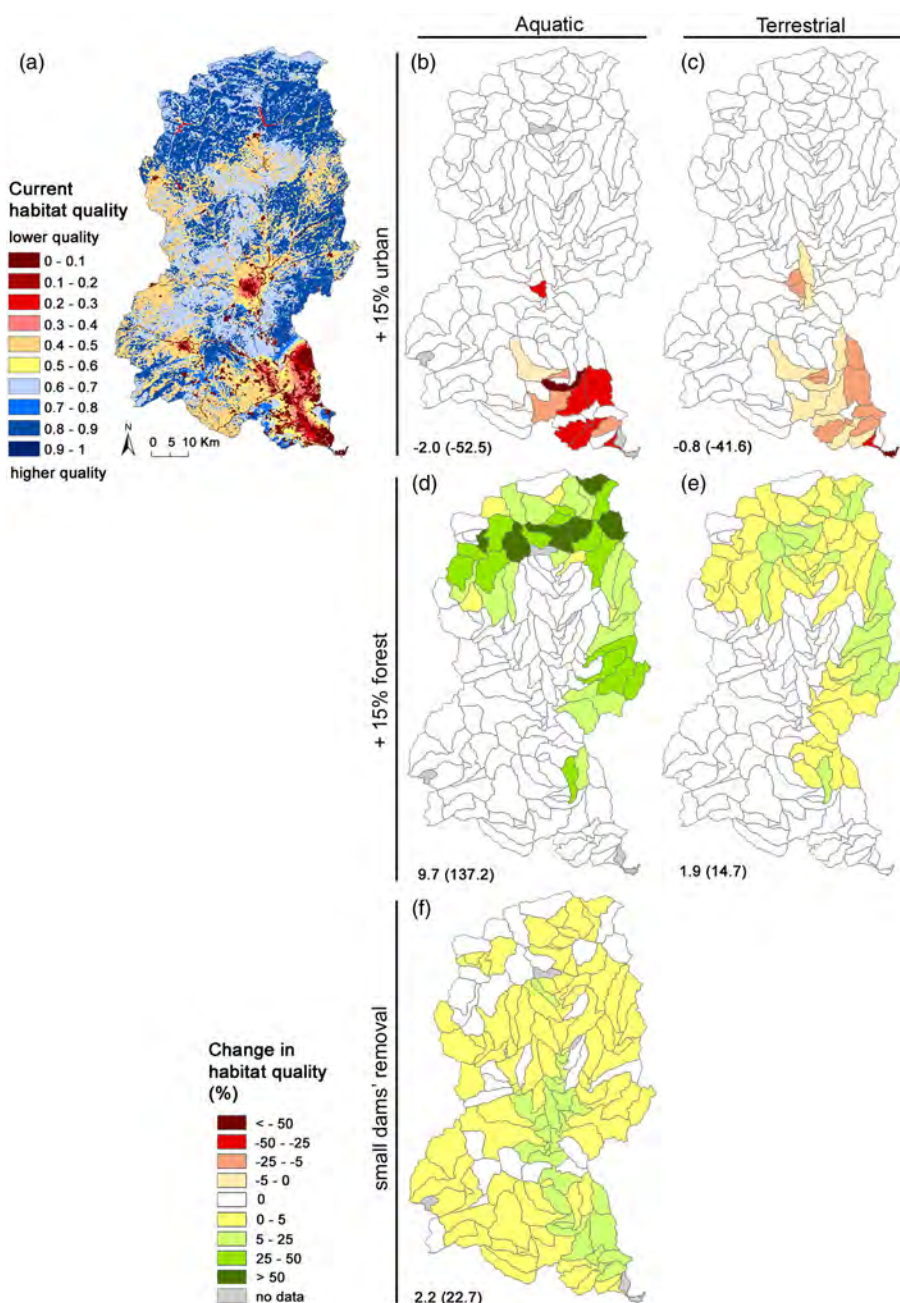
Fig. 2. Current habitat quality in the Llobregat River basin (a) and change in terrestrial and aquatic habitat quality at the sub-basin scale under different scenarios: increase of 15% urban land cover (b–c), increase of 15% forest land cover (d–e), and removal of small dams (only for aquatic) (f). Habitat quality scores differentiate areas according to their higher or lower habitat quality and, therefore, to their higher or lower capacity to host biodiversity. The number below each map corresponds to the percentage change in habitat quality. In brackets, maximal change per sub-basin. (For interpretation of the references to color in the text, the reader is referred to the web version of this article.)

parts of the basin (blue areas) had a higher habitat quality than areas closer to the river mouth (red areas), where the major urban settlements occur. Mean aquatic habitat quality in the basin was 25% lower than mean terrestrial habitat quality.

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

3.2. Habitat quality as a proxy for biodiversity

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

3.3. Model application to scenario analysis

The model proved to be sensitive to all analyzed scenarios, especially for aquatic habitat quality, which was always more impacted than
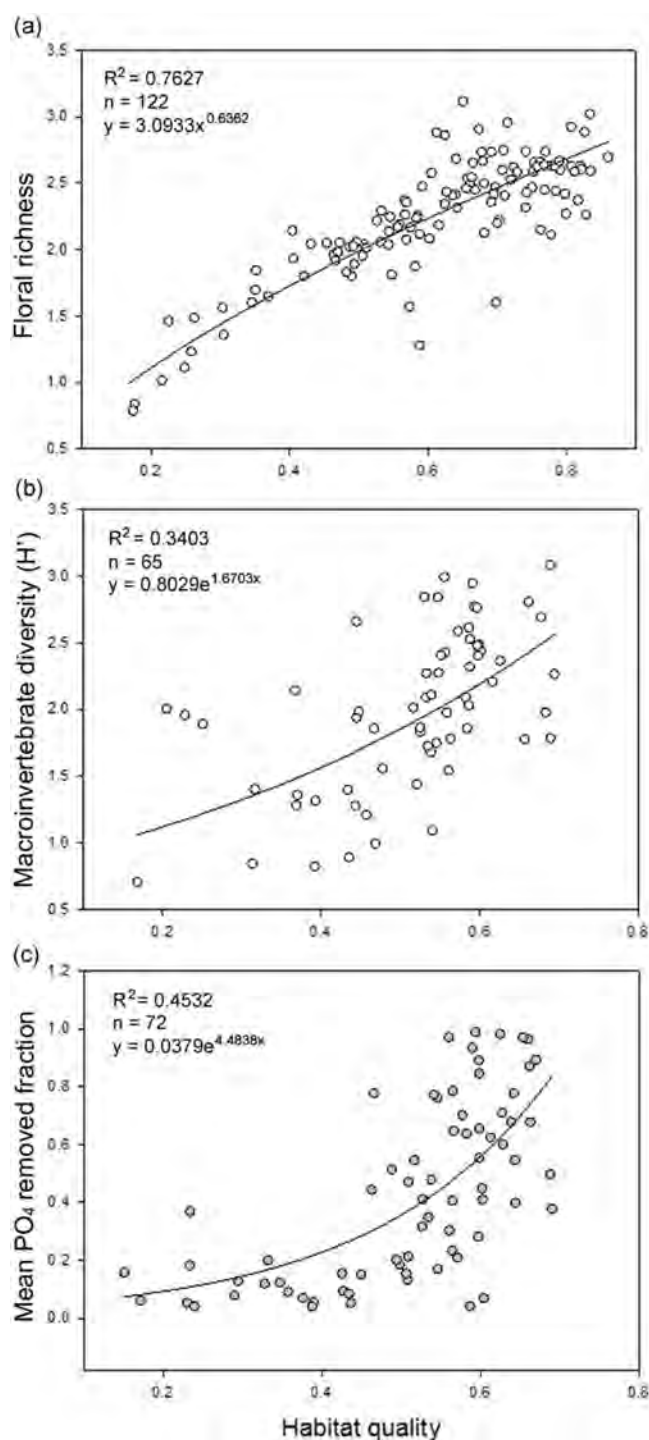
Fig. 3. Relationship between modeled habitat quality and observed indicators of biodiversity and ecosystem functioning in the Llobregat River basin: terrestrial habitat quality versus plant richness (a); aquatic habitat quality versus macroinvertebrate Shannon diversity (H') (b); aquatic habitat quality versus ecosystem functioning (mean in-stream phosphate removal) (c).

terrestrial habitat quality (Fig. 2). A scenario of 15% urban expansion (involving an increase of around 4450 ha of urban cover) caused a decrease in the mean habitat quality of the basin. Mean decreases in aquatic and terrestrial habitat quality were 2% and 0.8% respectively (Fig. 2b–c). Sub-basin habitat quality decreases of more than 25% were confined to the south-east portion of the basin for both terrestrial and aquatic ecosystems. The scenario of 15% increase in forest land cover (involving an increase of around 28,200 ha of forest) caused the highest change in

the average habitat quality of the basin. Mean improvements of aquatic and terrestrial habitat quality were 9.7% and 1.9% respectively (Fig. 2d–e). At the sub-basin scale, forest expansion increased the current habitat quality of aquatic ecosystems by more than 50% in some northern sub-basins. However, when looking at results per hectare, urban expansion generated a higher impact than forest expansion on both terrestrial and aquatic habitat quality. The average increase in aquatic habitat quality following small dams' removal was 2.2% (Fig. 2f). Dam removal at the sub-basin scale had the highest impact in the middle part of the basin, in the Llobregat River mainstem, where 5–25% increases in aquatic habitat quality were predicted.

4. Discussion

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

The correlation between observed indicators of biodiversity and modeled habitat quality in the study basin indicates an accurate direction of the response of biodiversity. However, we should take into account that no single biological indicator provides all the information needed to interpret the response of an entire ecosystem. A good fit was obtained for the terrestrial biodiversity indicator, which agrees with the relationship between habitat degradation and vascular plants identified elsewhere (Evans et al., 2011). The lower goodness-of-fit obtained for the aquatic biodiversity indicator (Fig. 3b) probably reflects the relevance of stream temporal dynamics, which is not considered in the model but plays a large role in determining the aquatic species at the moment of sampling. It may also be due to the selection of a single community (macroinvertebrates), which provides a limited representation of aquatic biodiversity. The number of samples and spatial coverage of macroinvertebrate data was lower than that for plant richness, and this also likely contributed to the lower goodness-of-fit between modeled habitat quality and observed aquatic biodiversity. Additionally, expert knowledge associated the highest aquatic habitat suitability to the highest-size stream reaches. This agrees with the work of Statzner and Higler (1985), who found that a higher plankton development in the lower stream reaches made the number of fish species increase, therefore influencing the diversity patterns of the whole community. This assumption does not entirely follow the River Continuum Concept that describes a maximization of biotic diversity in mid-reaches of streams as a result of the occurrence of the highest environmental variability (Vannote et al., 1980). On the other hand, studies exist that found no relationship between biodiversity and stream order (Statzner, 1981) or that diversity is almost constant throughout different orders (Minshall et al., 1982). The observed trend will probably depend on the particular characteristics of the study area, thus the assumption of either one hypothesis or another can affect the obtained results. In-stream nutrient retention was significantly correlated with the estimated aquatic habitat quality, indicating that the more degraded the habitats, the lower the species diversity and the lower the ecosystem functioning. Although we cannot infer a mechanism based solely on this correlation, it is consistent with the theory that biodiversity affects the functioning of ecosystems, with implications for the services that we obtain from ecosystems, such as water purification (Loreau et al., 2001; Hooper et al., 2005; Balvanera et al., 2006; Cardinale et al., 2012).

Habitat degradation in the Llobregat basin, as well as in many other multiple-use basins, was more pronounced near urban settlements and in the lower watercourses because of the accumulation of threats

coming from upstream. This supports previous findings identifying urban LU/LC as a major threat to natural ecosystems (Martinuzzi et al., 2014), and demonstrating the compounding of threats in the downstream direction along major river corridors (Vörösmarty et al., 2010). Urban settlements together with agriculture, livestock grazing, infrastructure, and extractive activities were also identified as the threats causing the highest habitat loss for terrestrial and freshwater species in Australia (Evans et al., 2011). Unlike our approach, that uses threats to obtain habitat quality (as a surrogate of species distribution), the approach followed by Evans et al. (2011) was based on species distribution as a surrogate for threats. In agreement with our results, they also found that freshwater species were more affected by threats than terrestrial species. The higher habitat degradation in aquatic ecosystems is certainly partly due to the reduction in habitat suitability values, but may be also an artifact of the approach followed, as aquatic habitat quality was affected by a higher number of threats than terrestrial habitat quality, coming from both land and water. In this work we assume aquatic threats to propagate only in the downstream direction. However, while this can work for the major part of considered threats, it overlooks the upstream impact of barriers such as weirs and dams that can also constrain the upstream movement of aquatic species. Although some parameter values used in the model (Tables 1 and 2) are case-specific, others can be transferred to other Mediterranean basins with similar characteristics when site-specific data are not available. This is the case of the habitat sensitivity to threats, S_{jr}, and the maximum distance of threat affectation, $Max.D$. On the other hand, the threat weight, W_r, depends on the importance of threats within the study area, which will be different in each basin. Only when general biodiversity is considered, can the values for habitat suitability, H_j, be transferred. Otherwise, specific values for the considered species need to be defined.

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

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

5. Conclusions

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

Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.scitotenv.2015.03.064.

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